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Edited by

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A REAPPRAISAL OF *DRYOPTERIS AFFINIS* SUBSP. *BORRERI* VAR. *ROBUSTA* AND NEW RECORDS OF *D. AFFINIS* SUBSPECIES IN EASTERN EUROPE

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ABSTRACT

Dryopteris affinis var. *robusta* is confirmed as being a variety of subsp. *borreri* as *Dryopteris affinis* (Lowe) Fraser-Jenkins subsp. *borreri* (Newman) Fraser-Jenkins var. *robusta* (Oberholzer & von Tavel ex Fraser-Jenkins) Fraser-Jenkins & Salvo.

Localities for var. *borreri* and var. *robusta* are listed from the author's collections in East Germany, Bulgaria, Czechoslovakia and Romania. In addition to subsp. *borreri*, subsp. *stilluppensis* also occurs as a rarity in Thuringia and Bulgaria. In the Northern Fagaras mountains of southern Romania var. *splendens* was found in addition to var. *borreri* and var. *robusta*; this is so far only published from Switzerland though Fraser-Jenkins (1982) suggests a wider range and states that it may be expected elsewhere. The diploid subsp. *affinis* var. *disjuncta*, known from Switzerland, West Germany, Austria and Italy, was also found in southern Romania, thus agreeing with Fraser-Jenkins' statement (pers. comm. 1984) that he has also found it in Britain, Spain, Portugal and France and expects it to occur anywhere throughout the range of subsp. *affinis* in sufficiently sheltered places.

INTRODUCTION

Fraser-Jenkins (1980, 1982) and in Dostál et al. (1984) has recognized in Europe (including Turkey and the Caucasus) the following subspecies and varieties of *Dryopteris affinis* (Lowe) Fraser-Jenkins:

D. affinis

subsp. *affinis* var. *affinis*

var. *azorica* Fraser-Jenkins

var. *disjuncta* (Fomin) Fraser-Jenkins

var. *punctata* Oberholzer & von Tavel ex Fraser-Jenkins

subsp. *borreri* (Newman) Fraser-Jenkins var. *borreri*

var. *pseudodisjuncta* (Oberholzer & von Tavel) Fraser-Jenkins

var. *splendens* (Ehrler) Fraser-Jenkins

subsp. *robusta* Oberholzer & von Tavel ex Fraser-Jenkins

subsp. *stilluppensis* (Sabranski) Fraser-Jenkins

Recent information about various of the subspecies and varieties is also given by Eschelmüller (1972), Schneller (1974), Eschelmüller & Schneller (1980) and Reichstein (1983).

Between the years 1975 and 1984 populations of *D. affinis* in East Germany were studied by the author. Material of this species was also collected in Czechoslovakia, Romania and Bulgaria. In the populations studied subsp. *borreri* and the taxon described as subsp. *robusta* are the most frequently occurring subspecies of *D. affinis*.

THE STATUS OF SUBSP. *ROBUSTA*

Whereas subsp. *affinis*, *stilluppensis* and *borreri* are usually relatively easy to differentiate, distinction between subsp. *borreri* and subsp. *robusta* is often difficult (as mentioned by Fraser-Jenkins 1982) and arbitrary and there does not appear to be a clear dividing line between them. From the following observations it appears that the status of the taxon *robusta* as a subspecies of *D. affinis* distinct from subsp. *borreri* is incorrect and it should be a variety of subsp. *borreri* (and see also Table 1).

TABLE 1.

	var. <i>borreri</i>	var. <i>robusta</i>
Features of distinction	leaves somewhat coriaceous, \pm thick or somewhat thin, mid- to light green; yellowish when young; pinnule (pinnalobes) -apices markedly squarely truncate, usually with entire or shallowly, squarely-lobed sides, the apices of the pinnules bearing \pm long acicular teeth often longer at the corners of the pinnule apices; indusia varying from relatively large at least when young, to small, thick or thin (but never as thick as in subsp. <i>affinis</i>), slightly brown to grey, lifting and shrivelling somewhat on ripening, often deciduous, usually with some being persistent.	leaves herbaceous to coriaceous, mostly relatively thin, mid- to light green; yellowish when young; pinnule-apices rounded, acute or subacute, if truncate then only near the frond apex, mostly with markedly incised to lobed, occasionally undulate sides, the lobes being \pm square, the apices of the pinnules bearing \pm long acicular teeth; indusia relatively small and thin, mostly light grey, on ripening lifting and shrivelling markedly, mostly deciduous.
habitat	In Europe widespread throughout many habitats and altitudes; in East Germany occurs most frequently in <i>Fagus</i> and <i>Fagus</i> -combined forests.	the same as var. <i>borreri</i> .
distribution	across the whole area of the species, except for all of Macaronesia (Azores, Maderia and Canaries), and rare in Portugal. The present author has collected it in Bulgaria, Czechoslovakia, Romania and East Germany. Fraser-Jenkins (1982) gives the whole range of the subspecies which is the same as that of the variety, based on his collection (in BM) and herbarium specimens seen.	the same as var. <i>borreri</i> .

- The two taxa are distinguishable only by the greater degree of lobing of the pinnules, the longer and more luxuriant pinnules and the larger frond of subsp. *robusta* (see Fraser-Jenkins 1980, 1982 and in Dostál et al. 1984); such features are of the type that may also occur in larger, better developed specimens of a single species as a result of greater growth.
- In spite of the relatively good separation between typical and well-developed plants of subsp. *robusta* (which are very frequently mistakenly identified as *Dryopteris x tavelii* Rothm.) and smaller or medium-sized subsp. *borreri* (also fairly often misidentified as *D. x tavelii*), transition forms between the taxa may be found in many populations, particularly those occurring partially in shade and partially in the open.
- Subsp. *robusta* and subsp. *borreri* appear not to occur growing together as distinctly separated taxa in the same habitat, but always to be connected by the intermediates mentioned.
- Cultivation of both taxa in approximately the same growing conditions show that the frond morphology of both taxa is able to approximate so nearly that it is difficult or almost impossibly artificial to tell one from the other.
- Subsp. *robusta* appears to be found dispersed throughout almost the whole range of the species (except Macaronesia and parts of North West Spain and Portugal) and in particular mirrors the range of subsp. *borreri* (see Dostál et al. 1984). Fraser-

Jenkins (pers. comm. 1984) adds that this is even more markedly obvious on a local level, particularly in Spain and Portugal where subsp. *borreri* is less common than it is elsewhere.

- Although requiring more study it seems fairly certain that the lack of pairing of chromosomes in the 16-celled sporangia resulting from the combination of different genomes present in subsp. *robusta* is the same as that in subsp. *borreri* (see Fraser-Jenkins 1982), whereas subsp. *robusta* and subsp. *borreri* show different pairing behaviour from subsp. *stilluppensis* (which shows approximately equal numbers of bivalents and univalents in 16-celled sporangia); subsp. *affinis* differs in being diploid.

Fraser-Jenkins (1982) has himself come to the conclusion that subsp. *robusta* merely represents luxuriant plants of subsp. *borreri*, and is probably best treated as a variety; he also considers this, and the other varieties treated for the purpose of Dostál et al. (1984) to be of little taxonomic importance, whereas the subspecies are far more significant. He points out (pers. comm. 1984) that intermediates occur between the varieties, and that the variation appears to arise from habitat differences, state of development of the plant and random variation genetically fixed by apomixis. Recently, Fraser-Jenkins and Salvo (1984) have made the new combination *Dryopteris affinis* subsp. *borrero* var. *robusta* (Oberholzer & von Tavel ex Fraser-Jenkins) Fraser-Jenkins & Salvo.

Although the subspecies are of considerable taxonomic significance, neither the present author nor Fraser-Jenkins (per. comm.) agree with Holub (1984) who continues to treat *D. pseudomas* (Woll.) Holub & Pouzar as a species, while ignoring subsp. *stilluppensis*. He also combines subsp. *robusta* as a subspecies of *D. pseudomas* which presumably arose from following Fraser-Jenkins' original erroneous publication. It seems likely that Holub has not realised how wide-spread subsp. *affinis* is in Europe and that it was previously included under *D. pseudomas*, or that he is not familiar with the three subspecies, which are sufficiently close that many botanists cannot identify them as yet. It is worth noting that Fraser-Jenkins (pers. comm.) also found subsp. *stilluppensis* in Czechoslovakia (Boskovice, N of Brno, CRFJ 4989, 15.7.1976) and it is at present impossible to exclude the occurrence there of subsp. *affinis* as a rarity. Study of the herbarium material at Prague under the name *D. pseudomas* will doubtless reveal more than one subspecies. Fraser-Jenkins (in prep.) intends to discuss the status, distribution, distinction and other details of the subspecies throughout their range, but he states that it is a common misconception that subsp. *borreri* is what used to be called *D. borreri* or *D. pseudomas*, while subsp. *affinis* is a little known taxon from SW Europe and Macaronesia; in fact the most extreme "*borreri*" (as opposed to *D. filix-mas*) is the widespread subsp. *affinis*.

NEW RECORDS OF *D. AFFINIS*

The following populations of subsp. *borreri* (both varieties) and other subspecies of *D. affinis* have been found by the author and specimens are deposited in the herbarium of the Arktisch-alpiner Garten und Herpetologische Versuchsstation, Karl-Marx-Stadt.

1. *D. affinis* subsp. *borreri*

1.1 East Germany

1.1:1 Thuringia

- Eisenach: "Landgrafenschlucht", 1 specimen seen, 25.9.1977, SJ-158: var. *robusta*.
- Winterstein: "Schwarzbachgraben", several specimens seen, 13.2.1977, SJ-167: var. *robusta*.

- Suhl: "Sperberggrund" below the "Schmücke", 3-5 specimens seen, 4.10.1975, SJ-165: var. *robusta*.
- Stützerbach near Ilmenau: "Marktal" (discovered by L. Meinunger), scattered, 11.10.1979, SJ-164: var. *robusta*.
- Steinach: "Leierloch", S slope of "Fellberg", 700m (discovered by L. Meinunger), 1 specimen seen, 20.8.1978, SJ-162: var. *robusta*.
- Steinheid: "Boosgrund" NNE of Theuern, 600m (see Meinunger, 1965), 5 specimens seen, 1.10.1983, SJ-351: var. *borreri*.
- Steinheid: "Schletzenbachtal" SSW of Steinheid, 700m (see Meinunger, 1965), 2 specimens seen, 1.10.1983, SJ-354: var. ?
- Lauscha: E slope of "Göritzberg", 640-650m (see Meinunger, 1965), ca. 5 specimens seen, 1.10.1983, SJ-347: var. *robusta* with transition to var. *borreri*.
- Lauscha: side valley of "Giftiggrund" S of "Pappenheimer Berg", 720m (see Meinunger, 1965), 3 specimens seen, 1.10.1983, SJ-349: var. *robusta*.
- Lauscha: western side valley of "Giftiggrund" ESE of Lauscha station, 630-660m (see Meinunger, 1965), 10 specimens seen, 1.10.1983, SJ-350: var. *borreri*.
- Goldisthal: "Grosses Langebachtal", 650m (see Meinunger, 1965), 4 specimens seen, 1.10.1983, SJ-352: var. *borreri*.
- Schalkau near Sonneberg: side valley of "Neundorfer Grund" S of Neundorf, shell limestone, 480m, 1 specimen seen (discovered by L. Meinunger), 1.10.1983, SJ-353: var. *robusta*.
- Burgk/Saale: cistern of Burgk castle, 1 specimen seen, 20.3.1981, SJ-368: var. *robusta*.
- Bürgel near Jena: "Waldecker Schlossgrund", 305-325m, more than 25 specimens seen, collected since 1975, SJ-166: var. *robusta* (see Fig. 1.).
- Stadtroda: wooded ravine S of Waltersdorf (see Marstaller, 1972), 3 specimens seen, 20.11.1981, SJ-361: var. *robusta*.



FIGURE 1 *Dryopteris affinis* subsp. *borreri* var. *robusta*: "Waldecker Schlossgrund" near Bürgel, Thuringia (DDR), Foto: S. Jessen, 1975.

- Stadtroda: "Glastal" E of "Hermannsmühle", 350m (see Marstaller, 1972), 4 specimens seen, 17.8. 1984, SJ-378: var. *borreri*.
- Stadtroda: "Heichbachgrund" NE of Karlsdorf, 310m (see Marstaller, 1972), 2 specimens seen, 18.8.1984, SJ-379: var. *borreri*.
- Eisenberg: "Grosser Tännigt" near Grüna (see Falkenberg, 1979), several specimens seen, 26.9.1981, SJ-364: var. *robusta*.
- Gera: "Teufelsgraben" SW of Reichardttsdorf (see Falkenberg, 1979), 7 specimens seen, 26.9.1981, SJ-143: var. *robusta*.
- Gera: stream ravine SW of Schafpreskeln (see Falkenberg, 1979), 5 specimens seen, 26.9.1981, SJ-362: var. *robusta*.
- Gera: "Türkengraben" E of Dürrenebersdorf (see Falkenberg, 1979), 17.7.1982, SJ-153: SJ-144: var. *robusta* (cytologically investigated by Mrs H. Rasbach, 21.8.1984: 123 bivalents).
- Gera: "Fuchsgraben" NW of Wolfsgefärth (see Falkenberg, 1979), 2 specimens seen, 17.7.1982, SJ-151: var. *robusta*.

1.1.2 Region of the Mulde (district Leipzig)

- Penig: sandy ground NE of Wernsdorf, 1 specimen seen, 23.6.1982, SJ-340: var. *robusta* or *borreri*.

1.1.3 Dresden district ("Sächsische Schweiz")

- Hohnstein: "Riesengrund", more than 10 specimens seen, collected since 28.3.1976, SJ-159: var. *robusta*.
- Hohnstein: "Kohlichtgrund", 2 specimens seen, 15.10.1977, SJ-160: var. *robusta*.
- Hohnstein: "Bärenhohlgrund", 4 specimens seen, 6.8.1978, SJ-161: var. *robusta*.
- Wehlen: "Diebskeller" ("Uttewalder Grund"), 4 specimens seen, 17.4.1981, SJ-360: var. *robusta*.

1.1.4 Halle district

- Thale: N slope of Bode valley near "Tiergarten Hexentanzplatz", 400m (discovered by L. Meinunger), 4 specimens seen, 17.6.1984, SJ-369: var. *robusta*.

1.2 Bulgaria

1.2.1 Pirin mountains

- SE Pirin: Brezniska valley NW of Goce Delcev, 1200m, 30.6.1976, SJ-169: var. *borreri*; 1800m, 5.7.1978, SJ-168: var. *robusta*.
- N Pirin: wood near Predel-Pass, 1200m, 1 specimen seen, 20.7.1981, SJ-331: var. *borreri*.

1.2.2 Rhodope mountains

- S of Plovdiv: ascent to "Prespa" (2000m) starting from Manastir, small wooded ravine, approx. 1525m, 1 specimen seen, 16.7.1983, SJ-346: var. *robusta*.

1.2.3 Balkan mountains

- Kalofer: Tuscha valley NNE of Kalofer, 1500m, 80-100 specimens seen, 16.7.1984, SJ-383: var. *robusta*.

1.3 Czechoslovakia

- Blansko, N of Brno: stream ravine NW of Dolni Lotha, 20.7.1977, SJ-170: var. *borreri*.

1.4 Romania

1.4.1 N Fagaras mountains

- Cirtisoara valley S of Cirta from 500-1200m, 15.8.1982, SJ-138, SJ-141: var. *borreri*; c. 500m, SJ-140: var. *robusta*; approx. 600-1200m, SJ-139: var. *splendens* (noticeably different from other varieties).
- Serbota valley S of Porumbaca de Jos, 500-1000m, 25.8.1982, SJ-133: var. *borreri*; var. *splendens* from 550-900m; var. *robusta* c. 550m in shady places.

1.4.2 Bucegi mountains

- W of Busteni: Alba valley, scattered, c. 950m, 27.8.1982, var. *robusta* and var. *borreri*.

2. *D. affinis* subsp. *stilluppensis*

2.1 East Germany, Thuringia (see Jessen, 1984).

- Steinach: "Schmidtsbruch" on the way to "Leierloch", about 600m, 12 specimens seen, 24.8.1980, SJ-163.
- Gera: "Grosser Tännigt" ESE of Gröna, 1 specimen seen, 26.9.1981, SJ-358.
- Gera: "Fuchsgraben" NW of Wolfsgefärth, 260m, 1 specimen seen, 17.7.1982, SJ-145.
- Triptis: wooded ground WNW of Hasla (see Marstaller, 1972), 4 specimens seen, 17.10.1981, SJ-142.
- Bürgel: between "Letsche" and "Mittelberg", 1 specimen seen (see Marstaller, 1972), 5.8.1984, SJ-375.
- 2.2 Bulgaria, Pirin mountains
 - N Pirin: Banderica valley near "Hütte Vihren", 1890m, 21.7.1984, SJ-384.
- 3. *D. affinis* subsp. *affinis*.
- 3.1 Romania, N Fagaras mountains
 - side valley of "Trans-Fagaras-way" and wooded slopes of the valley near Hotel "Bilea Cascada", scattered between 900-1250m, with subsp. *borreri* var. *borreri* and var. *splendens*, *D. remota*, *D. expansa*, *D. dilatata*, *Polystichum braunii*, *P. aculeatum*, *Athyrium distentifolium*, *A. filix-femina* etc; 16.8.1982, SJ-137: var. *disjuncta* (cytologically investigated by Mrs H. Rasbach, 21.8.1984: 82 bivalents).
 - Serbota valley S of Porumbaca de Jos, scattered between 650-1200m with subsp. *borreri*, *D. remota*, *D. expansa*, *D. dilatata*, *D. filix-mas*, *Athyrium filix-femina*, *Polystichum aculeatum*, *P. braunii*, *P. setiferum*; 24 & 25.8.1982, SJ-134: by comparison with named specimens sent by Prof T. Reichstein this is most probably var. *disjuncta*; cytological investigation has not yet been possible.

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ISOLATING MECHANISMS IN FOUR HIMALAYAN *DRYOPTERIS* SPECIES

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ABSTRACT

Four diploid sexual species of *Dryopteris* (*D. chrysocoma*, *D. caroli-hopei*, *D. nigropaleacea* and *D. cochleata*) are sympatrically distributed in NW Himalaya. A survey of a few selected localities in Mussoorie reveals no evidence of the presence of interspecific hybrids there. Habitat preferences of the sporophyte, and meiotic and spore-release periodicity, suggest that hybridisation may be minimised due to these isolating mechanisms. The indusium is involved in spore-release in addition to its role as a protective organ.

INTRODUCTION

The evolutionary history of a fern genus is learnt by study of populations of its species, particularly of the diploid sexual species, which may be taken as representing the basic diversity within the genus. Four diploid sexual species of *Dryopteris* Adanson [*D. chrysocoma* (Christ) C.Chr., *D. nigropaleacea* (Fras.-Jenk.) Fras.-Jenk. (in press),¹ *D. caroli-hopei*, Fras.-Jenk. (in press),² and *D. cochleata* (Ham. ex Don) C.Chr.] show sympatric distribution patterns in NW Himalaya and are clearly recognisable, with sharp morphological discontinuities. Despite the fact that natural populations of the first three species coexist in the general area under investigation, inter-specific hybrids have not been observed there, in contrast to the well-known high incidence of *Dryopteris* hybrids in Europe and North America (for a comprehensive review, see Lovis 1977). It should be noted though that several workers have suggested that hybrids in *Dryopteris* are frequent between species related to each other, with genomes in common, but rare between unrelated species, though exceptions exist in the indiscriminately frequent hybrids of the N. American species, *D. marginalis* (L.) Gray. Rarity of hybrids may therefore be expected between the unrelated species studied in the present paper. Only one such hybrid, *D. x wechteriana* Fras.-Jenk. (in press) (= *D. chrysocoma* × *D. nigropaleacea*) has been discovered (Fraser-Jenkins in press, Gibby in press). The absence or at least great scarcity of hybrids also suggests the possibility that the chances of hybridisation and subsequent survival of hybrid sporophytes may be further lowered by the existence of some hitherto unknown isolating mechanisms. As far as the author is aware, this aspect of Himalayan fern biosystematics has received far less attention than it deserves. The present study deals mainly with habitat preferences of the sporophyte plants and with meiotic and spore release periodicity, in the species mentioned.

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1. This species is common throughout the W Himalaya where it has long been included with other species under the name *D. odontoloma* (Moore ex Bedd.) C. Chr. However following the discovery of two cytotypes in the complex in the Himalaya (Mehra & Loyal 1965), Fraser-Jenkins (in press) has separated the diploid sexual plant as *D. nigropaleacea* and the mostly E Himalayan triploid apomictic plant as *D. juxtaposita* Christ, while true *D. odontoloma* is a triploid apomict apparently confined to South India.
 2. This species is separated from *D. marginata* (Wall. ex Clarke) Christ by Fraser-Jenkins (in press) and occurs throughout the Himalaya except in the far western part, whereas true *D. marginata* is confined to the East Himalaya.

MATERIAL AND METHODS

Three populations each of *D. nigropaleacea*, *D. caroli-hopei* and *D. chrysocoma* occurring within 2-3 miles of each other were selected for study at Mussoorie in NW Himalaya. Several populations of *D. cochleata* were studied within 5 miles radius of Mussoorie, in the foothills of Dehra Dun. The time of meiosis was recorded during a series of visits to the populations commencing in June. Indusial features related to spore-release, such as its size, cellular changes during ontogeny and features of the adult indusium were studied from whole mount preparations as well as from sectioned material stained in an aqueous solution of Ruthenium red. The period of maximum spore release was recorded between July and December.

OBSERVATIONS AND DISCUSSION

Altitudinal and habitat isolation. Of the 4 species, *D. nigropaleacea*, *D. caroli-hopei* and *D. chrysocoma* grow in the same general localities but in single-stands or in isolated populations between 2000-2500m. *D. chrysocoma* is essentially an inhabitant of open, steep, usually rocky, E-facing slopes, in clearings, or beside roads, on well-drained soil. The rhizome is short and ascendant, bearing a rosette of closely set fronds. In contrast, *D. nigropaleacea* and *D. caroli-hopei* grow on shaded forest floors where water run-off collects somewhat plentifully due to a thick cover of decaying plant materials, the chief tree component being *Quercus incana* Bartr., *Cornus macrophylla* Wall., *Aesculus indica* Colebr., *Ilex diphyrena* Wall., *Rhododendron arboreum* Smith and *Toona serrata* (Royle) M.J. Roem. *D. cochleata* is one of only two species of the genus in India (the other being *D. sparsa* (Ham. ex Don) O. Ktze) found in sub-montane forests from 800-1000m, and occurs throughout the Himalaya, except the far western part, and on mountains in the peninsula of India and in South India. It grows in different habitats from the other species, on soil along stream banks rich in clay or mixed clay and silt — typically an area affected by intense surface run-off.

D. chrysocoma receives direct sunlight for the greater part of the day; *D. nigropaleacea* and *D. caroli-hopei*, on the other hand, are adapted to partial shade and weak sunlight, though some populations of the former can tolerate relatively open spaces which are also more dry, for example in areas of biotic disturbance such as where grazing or felling has occurred. In such populations the plants develop a somewhat stiff-textured lamina, and sporulation in these semi-xeric individuals may occur slightly earlier than in those occupying more shaded and less dry localities.

As in *D. chrysocoma*, *D. nigropaleacea* has a short, ascendant rhizome bearing closely-set, medium-sized fronds. By contrast *D. caroli-hopei* has very large fronds up to 1.5m and the plants inhabit more humid environments with a damp substratum. The rhizome is horizontal and somewhat creeping, with slightly distantly-placed fronds.

It is clear that the sporophytes of all four species have specific ecological requirements which do not normally permit intermixing of the species in a given locality, though it may be expected that in certain transition habitats, such as the secondary environments at the edges of roads and clearings, they may become closely juxtaposed.

Frond life-span. At the onset of the monsoon rainy season in June and July, *D. chrysocoma* produces a few vegetative fronds before the fertile ones. All the fronds produced during one growth season enter senescence and then die during the late Autumn; however they remain attached to the rhizome apex in a brown and semi-dried-up condition and the fertile ones release the spores during and after the Winter snowfall — a situation comparable with *Matteuccia struthiopteris* (L.) Tod. in New England (Klekowski, 1979). In contrast the fronds of *D. nigropaleacea* and *D. caroli-hopei*, are biennial, i.e. the fronds may remain green for at least two years.

In virtually all the fertile fronds of *D. nigropaleacea* examined, the soriferous pinnae are restricted to the upper half of the lamina; this may be connected with more efficient spore dispersal. *D. cochleata* has dimorphic fronds; the more upright fertile fronds have a distinctly narrower lamina and a longer stipe than the vegetative fronds. In all the populations examined, the vegetative fronds are produced during the monsoon, from July onwards and the fertile ones during October-November.

Meiotic periodicity. Table 1 shows onset of meiosis for *D. nigropaleacea* in June during pre-monsoon showers, for *D. caroli-hopei* and *D. chrysocoma* in July during the monsoon, and for *D. cochleata* in October with low temperature, low humidity and no rainfall.

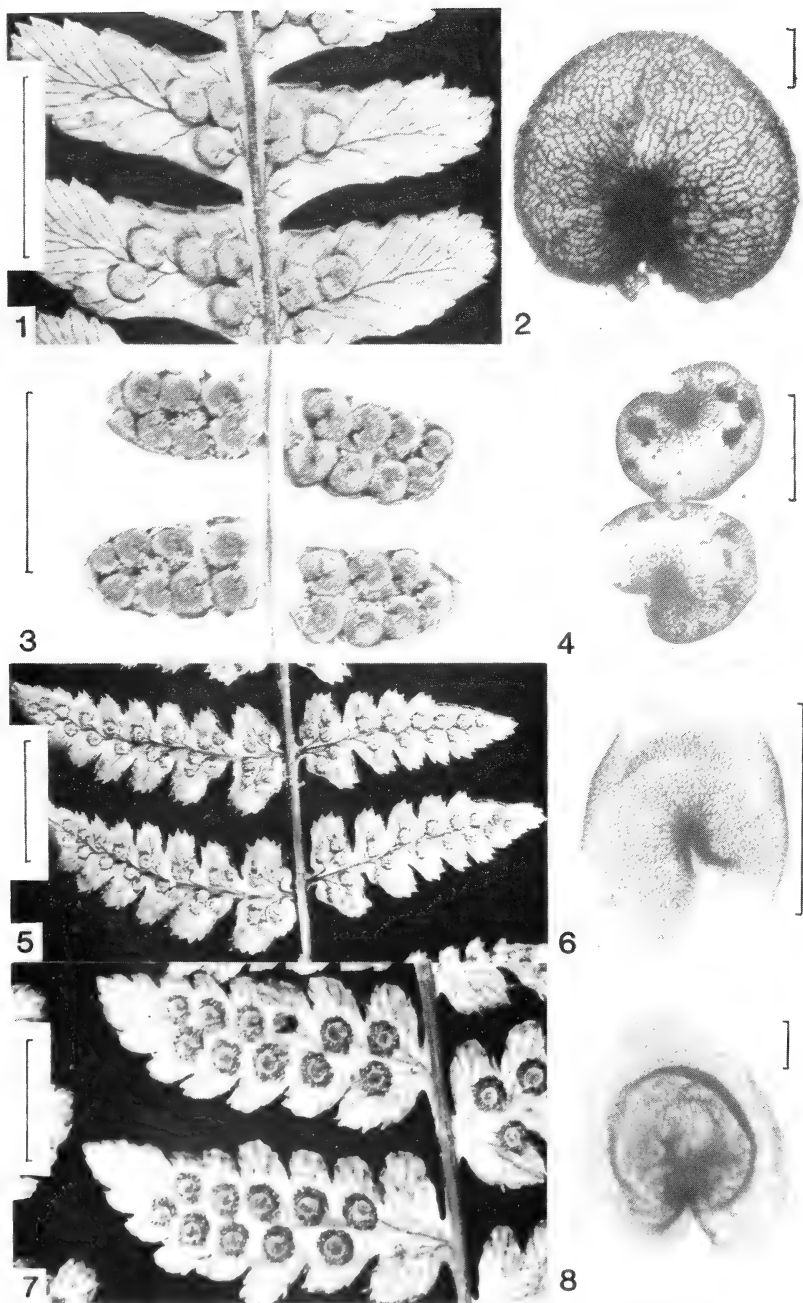
Indusial features. Study of the following indusial features provides information relevant to the spore-release periodicity: (a) Growth rate in relation to receptacular and sporangial development, (b) size and cellular configurations at maturity and (c) the timing and extent of pectin deposition on the cell walls.

TABLE 1. Comparison of the four *Dryopteris* species.

Species	Frond	Onset of meiosis	Maximum spore-release	Indusium		Sporangium	Spores
				Life-span	Size		
<i>D. nigropaleacea</i>	Monomorphic, biennial	June	Early August	Short-lived	874 x 600µm	87 x 110µm	20.5 x 16.5µm
<i>D. caroli-hopei</i>	Monomorphic, biennial	July	Late August	Short-lived	969 x 720µm	97 x 128µm	20 x 13.5µm
<i>D. chrysocoma</i>	Monomorphic, annual	July	December-January	Persistent	1150 x 890µm	160 x 200µm	40 x 30µm
<i>D. cochleata</i>	Dimorphic, annual	October	Early December	Persistent	1000 x 880µm	155 x 180µm	39 x 29µm

In *D. chrysocoma*, the prominent thick sorus remains fully closed, up to and long after spore formation (Figs. 1, 2). As Fig. 2 shows, *D. chrysocoma* has the largest indusium of the species investigated, with the incurved margin more-or-less reaching the receptacular base below the sporangia. Except for the marginal cell layers, which continue to divide by both anti- and periclinal divisions, all the lower-lying cell layers enter an expansion phase during the growth of the indusium, becoming markedly rectangular. A few basal, first-formed cell layers develop undulate walls which occur only in the oldest part of the indusium. In the other three species, virtually all the cell layers develop characteristic undulate walls, and once cell expansion and undulation have set in, further cell formation ceases. In *D. chrysocoma*, the indusium develops precociously, i.e. much earlier and faster than the subtending sporangia and its growth continues by cell-division and expansion for an appreciably longer period of time than that in the other species. An apparent advantage that accrues from this growth pattern is that the empty space between the developing sporangia and the indusial cover always contains humid, saturated air or even becomes filled with minute water droplets, thus preventing desiccation. Deposition of pectin on the indusial cell walls is meagre or, in most of the cases examined, does not even occur at all. In *D. cochleata* (Figs. 3, 4) the adult indusial form and its growth pattern is similar to that in *D. chrysocoma*, except that pectin deposition is far greater, the end result bearing a striking resemblance to collenchyma thickenings; the adult indusium of *D. cochleata*, though curved down at the sides, also has markedly less inflected margins which lift very slightly to expose the lowermost edge of the sporangial mass, on ripening.

The thin, short-lived indusia of *D. nigropaleacea* (Figs. 5, 6) and *D. caroli-hopei* (Figs. 7, 8) are flap-like (more-or-less flat), or helmet-shaped (curved slightly over the top of the sorus), respectively. Differentiation of their constituent cells by means of vacuolation and expansion is completed in a relatively shorter period of time than in the two former species, with indusial cell-division in a sorus ceasing well before the development of all the sporangia in that sorus. Thus, in both these species, where the

FIG. 1. *D. chrysocoma*, part of fertile frondFIG. 2. *D. chrysocoma*, indusium.FIG. 3. *D. cochleata*, part of fertile frond.FIG. 4. *D. cochleata*, indusia.FIG. 5. *D. nigropaleacea*, part of fertile frond.FIG. 6. *D. nigropaleacea*, indusium.FIG. 7. *D. caroli-hopei*, part of fertile frond.FIG. 8. *D. caroli-hopei*, indusium.

(Figs. 1, 3, 5, 7 Scale represents 1cm; Figs. 2, 4, 6, 8 Scale represents 0.5mm.)

indusial margins do not curve down around the sporangia, the stage is set for spore release as soon as the only partially protected sporangia reach maturity during the wet mid to late monsoon weather of August to September. In the populations of *D. nigropaleacea* examined, maximum spore release by sporangial dehiscence occurs by early August.

Spore release. Although the period during which meiosis occurs in *D. chrysocoma* and *D. caroli-hopei* is practically the same, spore-release in the former is postponed until the Winter which is a cold, dry period in the West Himalaya, or until early Spring — a situation akin to that in the somewhat unusual overwintering fern fronds in some temperate species of the genus (Farrar 1976). Delayed spore release is associated with frond senescence during the period of low temperature. Fronds of *D. chrysocoma* which have not experienced senescence under low temperature, for instance collections made by the author in August-September in the 1950s, failed to release their spores despite drying as herbarium specimens. In this species both senescent state and the persistent indusium seem to play a role in spore-release. Apart from wind dispersal the snow, or water from streams passing over the rocks it often grows on, may carry spores or sporangia in this species.

The possible adaptive significance of spore-release during the dry, cold season in *D. chrysocoma* and *D. cochleata* can be considered. The spores of *D. chrysocoma* (c. $40 \times 30\mu\text{m}$) and *D. cochleata* (c. $39 \times 29\mu\text{m}$) are distinctly larger and have a thicker perine than those of *D. nigropaleacea* (c. $20.5 \times 16.5\mu\text{m}$) and *D. caroli-hopei* (c. $20 \times 13.5\mu\text{m}$). One possible advantage of the large spore-size is that the larger quantity of food reserves stored in them could allow better establishment of the gametophytes before the rising temperatures of early summer, or could help the spores to remain alive in a dormant state during the considerable period they are retained on the frond in a ripe state in late Autumn and early Winter. It seems likely that the prothalli and sporelings of *D. chrysocoma* may be able to escape natural competition from the flush of growth of prothallial vegetation belonging to species from numerous genera during the monsoon, though further study is required into the natural growth period of its gametophytes and sporelings in the field. In the case of *D. cochleata*, the prothalli and sporelings (young sporophytes) may escape the intense heat and dry winds of summer that occur in the submontane region, and it is perhaps no coincidence that *D. cochleata* is in general a SE Asian and more southerly, lower level species, whereas the other species considered are all Sino-Himalayan species (see Fraser-Jenkins in press).

THE IMPORTANCE OF ISOLATING MECHANISMS

Finally, if it is correct that isolating mechanisms have been the cause of rarity of F₁ hybrids (as opposed to allopolyploids) in the Himalaya, the role of the different environments, and the past history of the Sino-Himalayan element of the genus will have to be considered and studied. As regards isolating mechanisms in plants in general, Stebbins (1950) has stated that "hybridisation between well established species in a stable environment will have no significant outcome — or will be detrimental to the species population — hence the importance of isolating mechanisms". The presence of numerous spontaneous hybrid plants competing with the parental species is clearly detrimental, and it is clear that resulting allopolyploid species can often out-compete the ancestral species unless the ecological requirements of the ancestors are so distinct that the allopolyploid species can themselves find an intermediate and distinct ecological niche. In *Dryopteris* many such allopolyploids (including apomicts) occur in the Sino-Himalayan region along with a number of sexual diploid species, all being more-or-less isolated by their ecology or by other factors such as those discussed in this paper. Previous reports of high percentages of diploid sexual species certainly do not hold true for this genus in

this region, as only two fifths of the 48 Indo-Himalayan species known at present are sexual diploids (see Fraser-Jenkins in press). However it is certainly true that hybrids of *Dryopteris* in the area are uncommon; Fraser-Jenkins (in press) reports nine hybrids from the Indo-Himalaya almost all of which are known from only one plant. One of these hybrids, *D. x wechteriana*, is between two of the species studied in this paper, *D. chrysocoma* × *D. nigropaleacea* (Gibby in press), and was growing as a single plant on a roadside above Simla, Himachal Pradesh. Analysis by Fraser-Jenkins (pers. comm. 1983) of the kind of hybrids of *Dryopteris* reported from N. America (as detailed by Widén, Britton, Wagner & Wagner 1975) and from Europe (as detailed by Fraser-Jenkins 1982, and Dostál et al 1984) reveals that, with certain exceptions, hybrids between species that are not related by having genomes in common are usually extremely rare, if they occur at all, whereas "backcross" hybrids, between species with a genome in common are frequent (see also Fraser-Jenkins, Reichstein & Vida 1975). It would seem likely that the scarcity of hybrids in the Himalaya may be attributed to a similar isolation barrier between unrelated species. It does not seem likely that many of the seven tetraploid sexual species (a very low number) occurring in the Indo-Himalaya could occur sympatrically with any proposed ancestral sexual diploid species, which thus reduces the possibility of triploid "backcross" hybrids occurring, in contrast to the situation in N. America and Europe. Nearly half of the Indo-Himalayan *Dryopteris* species are apomictic, and hybrids involving these may be expected to be difficult to recognise.

ACKNOWLEDGEMENTS

I am grateful to Mr C.R. Fraser-Jenkins, British Museum (Natural History), London, for help with the nomenclature and useful discussion and comments on the systematics of Himalayan species of *Dryopteris*. For the financial grant which made the field trips possible, I thank the Dean, University Instruction, Panjab University, Chandigarh.

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ANOMALOUS FRONDS AND VENATION IN *POLYBOTRYA CERVINA*

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ABSTRACT

Aberrant fronds in *Polybotrya cervina* are figured and described. In them the venation is anastomosing and complex as compared with that of normal fronds of this species in which the veins are simply forked and joined at the distal ends by a single commissural vein.

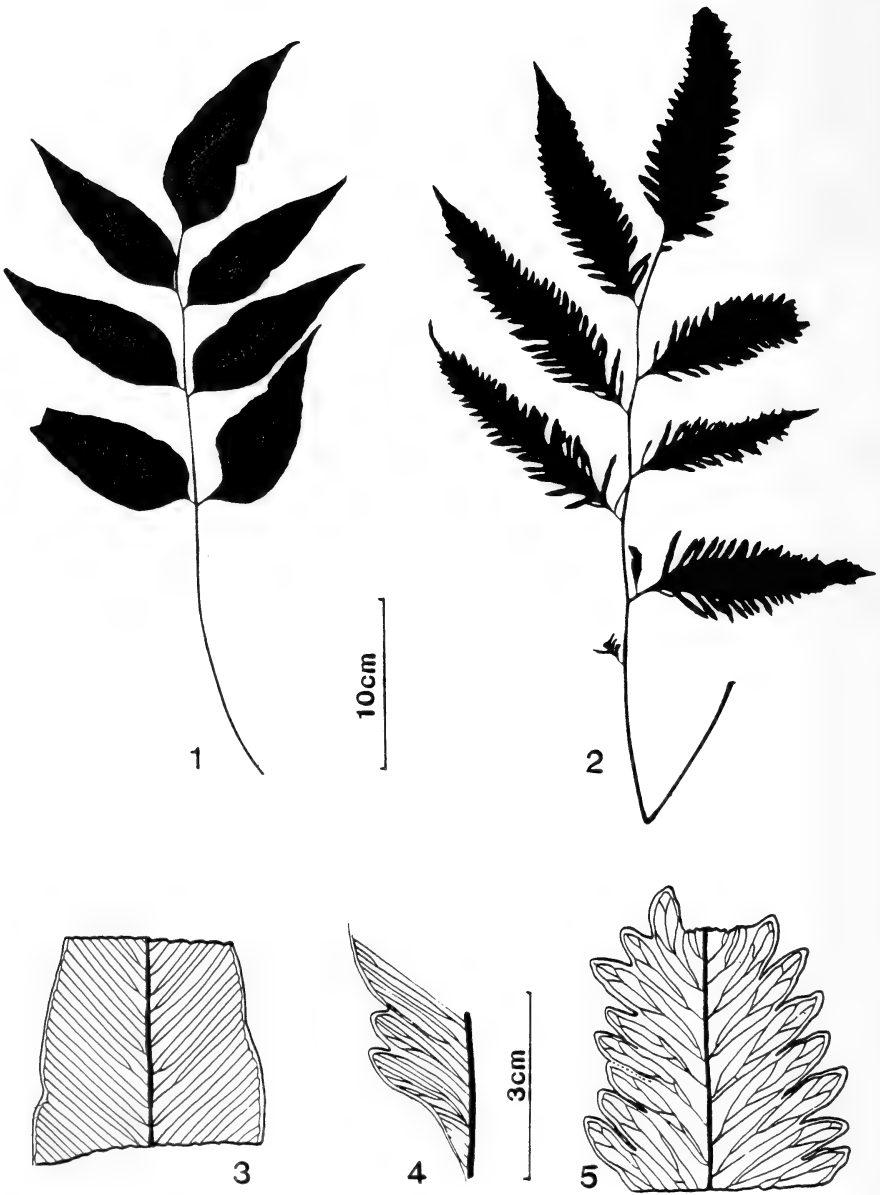
INTRODUCTION

Polybotrya is a genus of Caribbean, Central and South American ferns, comprising some 40 or more species. Most of the species are scandent on trees, despite having established themselves at first on the ground and with which they do not subsequently lose contact. Like some other scandent ferns such as *Maxonia apiifolia* (Sw.) C. Chr. the terrestrial rhizome is relatively thin but thickens considerably in its scandent phase (Walker 1972). Marked dimorphism of the fronds is characteristic, the sterile ones being simply pinnate to quadripinnate. In the fertile fronds the lamina is greatly reduced or absent, the segments being covered to a greater or lesser extent by acrostichoid sporangia. Venation of the sterile fronds is very variable, ranging from being completely free as in *P. caudata* Kze (Fig. 11) to completely anastomosing as in *P. serratifolia* (Fée) Kl. (Fig. 10) but without included veinlets in the areoles. A wide range of frond form and venation is illustrated in Tryon and Tryon (1982).

Polybotrya cervina (L.) Kaulf. is somewhat anomalous in the genus in having a rhizome with very limited growth with the result that the plant is not normally scandent but tends to grow on the forest floor, on rocks or on fallen tree trunks, etc. It is also very amenable to cultivation and makes an excellent pot plant. The simply pinnate leathery fronds (Fig. 1) have simple or once-forked veins which are connected at their distal ends by a marginal commissure (Fig. 3). The fertile fronds are more complex in their general architecture (Fig. 8) being bipinnate and covered with naked sporangia. The rather isolated position of *P. cervina* has led to its recognition as a distinct genus *Offersia* by Raddi. Occasionally anomalous fronds with aberrant venation are produced by this species which show similarities to frond form and venation patterns seen in other species of *Polybotrya* and these form the subject of the present paper.

ANOMALOUS FRONDS

Anomalous fronds have arisen from time to time on plants of *P. cervina* from Jamaica and Trinidad which are in cultivation at Newcastle. These are usually photosynthetic fronds showing various depths of lobing and one such is shown in Fig. 2. In this particular frond a few sporangia were also produced on the back of the lowest pinna pair. A feature of such fronds is that they are of sporadic occurrence and the next fronds that are produced are all normal, thus the phenomenon is not genetic in the sense seen in the leaf 'sports' so beloved of some fern enthusiasts. However, over the course of years several anomalous fronds may be produced from time to time by the same plant. A very interesting series of specimens in the British Museum (Nat. Hist.) consists of a number of fronds gathered by John Smith between 1849 and 1859 from a (presumably) single plant grown at Kew, some of which are illustrated here and showing a wide range of variation.



FIGS. 1-5 *Polybotrya cervina*. Fig. 1 normal sterile frond; Fig. 2 anomalous frond; Fig. 3 normal venation; Fig. 4 venation in shallowly lobed frond; Fig. 5 venation in deeply lobed frond.

One sheet (not illustrated) shows parts of two fronds, one with normal pinnae (A) and the other with lobed pinnae (B) which parallel my fronds shown in Figs. 1 and 2. This sheet is labelled "v.v. Hort Kew 1857. A & B from the same sarmentum" (sarmentum refers here to the rhizome). A complete mixture of normal-shaped and deeply lobed sterile pinnae together with normal fertile pinnae occur together in a single frond gathered in 1856 (Fig. 6) whilst an 1849 specimen consists of an otherwise normal fertile frond in which the ends of the lowest two pairs of pinnae are broadened, lobed and photosynthetic (Fig. 7); Figs. 8 and 9 show two fertile fronds from the same plant gathered in 1859 in which the secondary pinnae are almost completely suppressed, appearing on only a few primary pinnae as undulations.

Such anomalies as have been found at Newcastle and Kew are not merely the chance effects of cultivation, similar specimens having been also found in the wild as attested to, for example, by a specimen (Johnston 185) collected from the top of Tucuche in Trinidad on 29th April, 1945 (BM).

ANOMALOUS VENATION

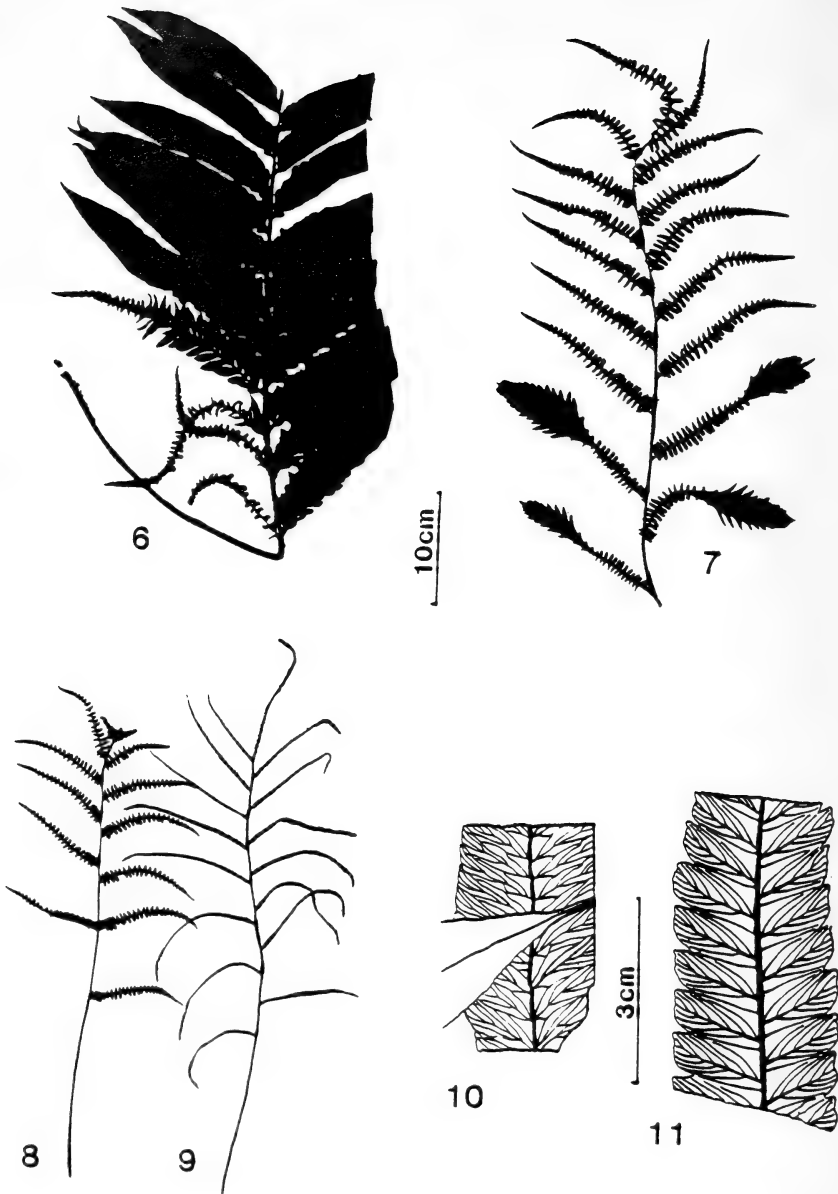
One of the most remarkable features about these anomalous fronds is the effect that lobing of the pinnae has upon the pattern of venation. The venation changes radically to produce something totally different from that which might be expected to follow on a fairly simple change in outline of the pinna margin. Very shallow lobing such as is seen in Fig. 4 leads to the normal venation (Fig. 3) being more or less maintained except that the marginal commissure is interrupted by the lobing. In the case of deeper lobing however such as seen in the frond illustrated (Fig. 2) the venation becomes completely reorganized, giving rise to a totally different pattern from that found in normal entire fronds. Thus, not only is each lobe provided with its own set of veins but these anastomose completely and also branch quite profusely giving rise to a series of areoles four or five deep and lacking any included veinlets (Fig. 5). This approaches very closely the venation pattern seen in a species such as *P. serratifolia* (Fig. 10), the main difference being that in the latter the veins are not divided up into blocks as in anomalous *P. cervina*. It should be pointed out here that there is no lobing in *P. serratifolia* to cause such a division.

DISCUSSION

Extrapolation from teratological forms is always a hazardous venture, especially as to the direction in which the change has occurred. Nevertheless, one may suggest that *P. cervina* is a simplified derived member of *Polybotrya*, simplified not only in frond morphology but also in venation. The specimens do however indicate quite clearly that in this species at least, relatively simple changes in pinna morphology lead to changes in venation of a most profound nature, of the order of magnitude that in most ferns would place two plants having the venation shown in Figs. 3 and 5 in different genera. It points the lesson that the value of venation as a character must be separately assessed for each genus or group of genera and that it does not have an equal value in every case.

ACKNOWLEDGEMENTS

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FIGS. 6-9 *P. cervina*, anomalous fronds in Herb.J.Smith, Figs. 10-11 venation patterns in *Polybotrya*. Fig. 6 collected 1856; Fig. 7 collected 1849; Fig. 8 collected 1859, normal fertile frond; Fig. 9 anomalous fertile frond collected from same plant as in Fig. 8; Fig. 10 venation in *P. serratifolia*; Fig. 11 venation in *P. caudata*.

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CYTOLOGY AND TAXONOMY IN WOODSIACEAE*

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ABSTRACT

Chromosome counts of ten species of Chinese Woodsiaceae are reported. Chromosome numbers and morphological comparison support the proposal that the family Woodsiaceae should be divided into three genera, and the genus *Woodsia* into five sections. Base numbers of $x = 33$ in *Protowoodsia* and $x = 41$, 39 and 38 in *Woodsia* may indicate relationship with *Sticherus* ($x = 34$) and *Dicranopteris* ($x = 43$) in Gleicheniaceae. Woodsiaceae may be derived from the common ancestor of *Sticherus* and *Dicranopteris*.

INTRODUCTION

The family Woodsiaceae includes about 30 species, mainly distributed in the northern temperate zone. Thirteen species (Table 2) have been previously investigated cytologically; the gametic chromosome numbers were found to be 41, 39, 38, 33 or their multiples. The present paper provides chromosome counts of ten species from China, of which nine represent new counts (Table 1).

According to Ching (1978), Woodsiaceae includes three genera, *Woodsia*, *Protowoodsia* and *Cheilanthesopsis*, the latter two being monotypic with distinct morphological characters. Cytological evidence for this classification, and the division of *Woodsia* into Sections, is discussed.

MATERIAL AND METHODS

All the experimental material was collected wild in China (Table 1). Young fertile fronds were fixed in 1:3 acetic acid: alcohol for 24 hours or more. Spore mother cells (SMCs) were examined using the squash technique of Manton (1950). Voucher specimens have been deposited at the Institute of Botany, Academia Sinica, Beijing (PE).

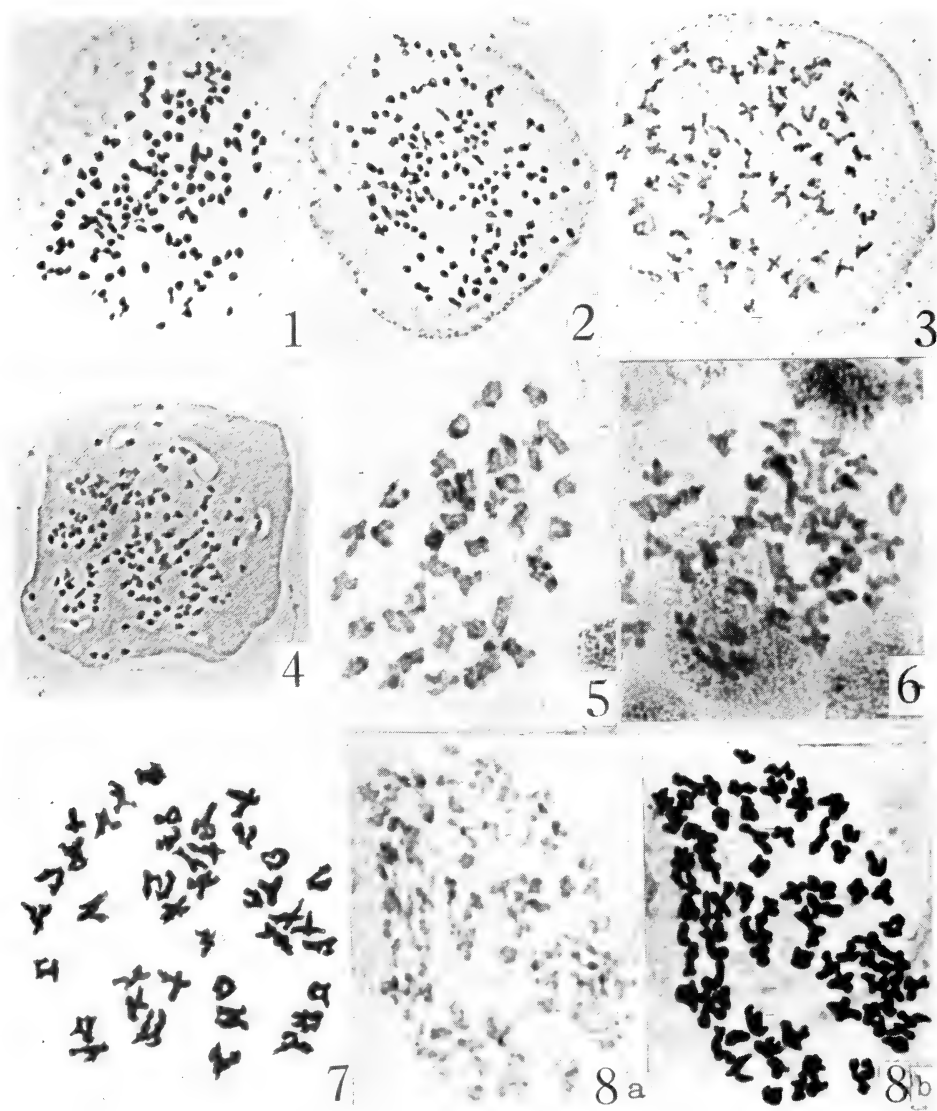
RESULTS

The chromosome counts of ten species of Chinese Woodsiaceae are summarized in Table 1. Photomicrographs are shown in Figures 1-12.

1. *Woodsia lanosa* Hook. A small fern distributed in SW China, over 3000m in rock crevices; an octoploid, $n = 164$. Type from Sikkim Himalaya.

2. *W. andersonii* (Bedd.) Christ. A small fern distributed in W China, over 3000m in rock crevices. Type from Kumaon, Sikkim Himalaya. The fronds vary morphologically with different habitats. Cytologically it is unique: there are 16 SMCs per sporangium and 164 bivalents at late diakinesis, but from metaphase 1 to the formation of young spores meiotic division is highly irregular in most sporangia, with univalents at metaphase 1 and 2, lagging chromosomes and chromosome bridges at anaphase 1 and 2. Finally, many of the sporangia contain less than 64 spores, and these are highly irregular in size (30-70 μ m diam.) and shape. The irregular meiosis is similar to that seen in hybrids. The count of $n = 164$ indicates that it is an octoploid, and it may be a segmental allopolyploid derived from two closely related parents, probably *W. macrospora* C. Chr. and *W. lanosa* from morphological comparison. However, this needs to be confirmed in further study.

*This is part of a thesis submitted as partial fulfillment for the degree of Master of Botany at the Institute of Botany, Academia Sinica.



FIGURES 1-12 Photographs from aceto-carmin squash preparations of SMCs at diakinesis or first metaphase of meiosis in ten species and two varieties of Chinese Woodsiaaceae (magnifications in brackets).

FIGURE 1. *Woodsia lanosa* $n = 164$ (c. 1000).

FIGURE 2. *W. andersonii* $n = 164$ (c. 1000).

FIGURE 3. *W. rosthorniana* $n = 82$ (c. 1200).

FIGURE 4. *W. cycloloba* $n = 164$ (c. 1000).

FIGURE 5. *W. ilvensis* $n = 39$ (c. 1800).

FIGURE 6. *W. polystichoides* var. *polystichoides* $n = 41$ (c. 1500).

FIGURE 7. *W. polystichoides* var. *sinuata* $n = 41$ (c. 1500).

FIGURE 8a, b. *W. subcordata* $n = c. 80$ (c. 1200).

*Figures 8b, 9b, 11b and 12b are inked in; all the rest are original photographs.

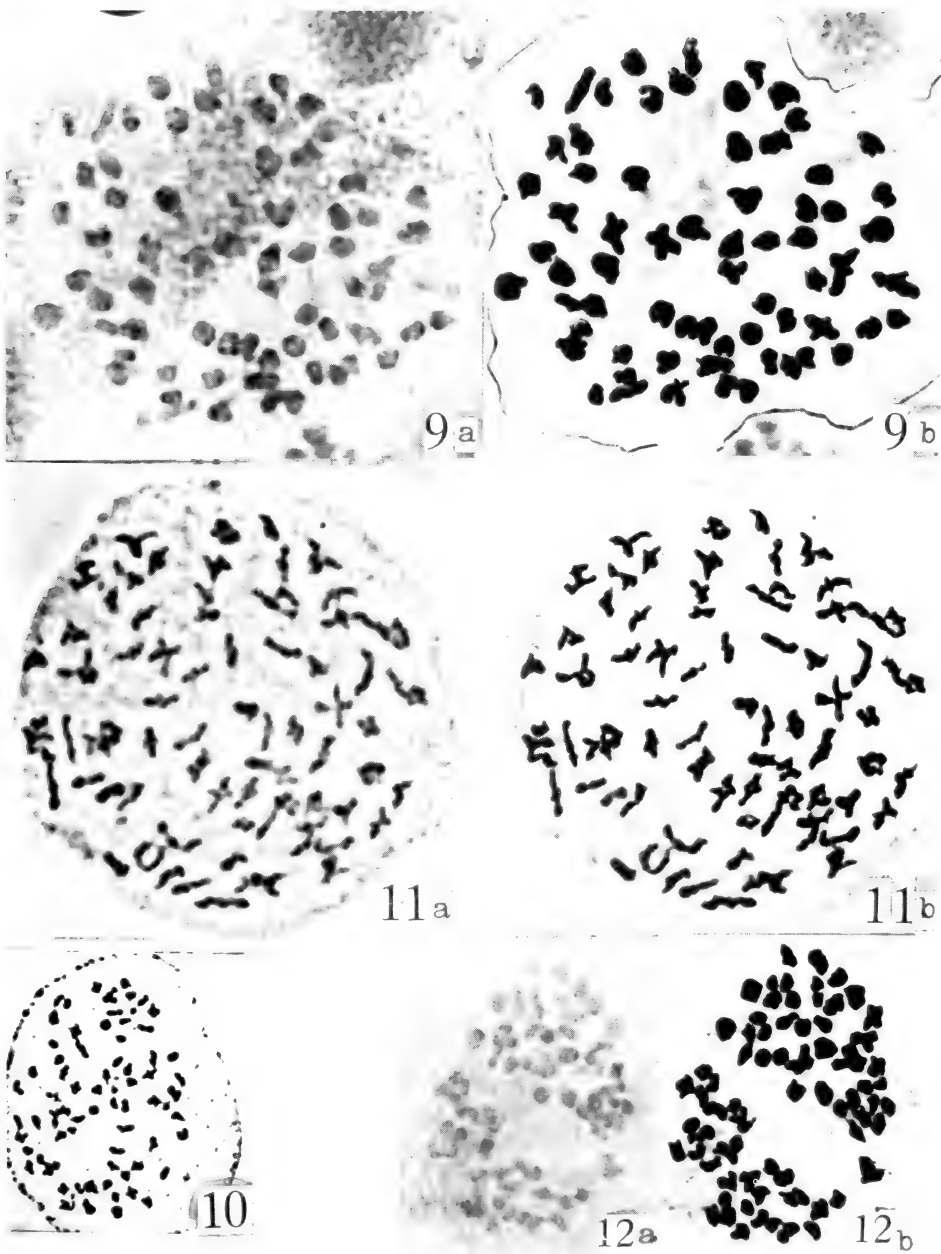


FIGURE 9a, b. *Protowoodsia manchuriensis* $n = 66$ (c. 2000).
FIGURE 10. *Woodsia elongata* $n = 82$ (c. 1000).
FIGURE 11a, b. *Cheilanthopsis indusiosa* $n = 74$ (c. 1800).
FIGURE 12a, b. *Cheilanthopsis indusiosa* showing 74 bivalents divided into two groups at diakinesis (c. 1200).

3. *W. rosthorniana* Diels. A medium-sized fern distributed in W and N China. A tetraploid, $n = 82$. Type from Sichuan.

4. *W. cyclobola* Hand-Mazz. A small fern distributed in W China over 3000m, in rock crevices. Octoploid, $n = 164$. Type from the Mekong-Salwin divide, NW Yunnan.

The above four species are all polyploids with the basic chromosome number $x = 41$.

5. *W. ilvensis* R. Br. A medium-sized fern widely distributed in the N hemisphere. It is diploid with $n = 39$ in the material from Heilongjiang Province, NE China. Two different chromosome numbers have been reported for this species, $n = 41$ and $n = 39$ (see Table 2). It is not certain whether some of the counts are wrong, or whether there really are two cytotypes within this one species.

6. *W. polystichoides* Eat. var. *polystichoides*. A medium-sized fern distributed in E Asia, especially throughout China. The fronds vary much in size and shape in different localities. A diploid, $n = 41$. Type from Japan.

7. *W. polystichoides* Eat. var. *sinuata* Hook. A medium-sized fern from Liaoning, Shandong, and Hebei Province. Diploid, $n = 41$. Type from Talianwan, Liaoning.

8. *W. subcordata* Turcz. A medium-sized fern from NE Asia, namely Siberia, USSR, Mongolia, Korea, Japan and N China. The pinnae vary in shape. Type from N China. There are about 80 bivalents at metaphase 1 (Figure 8; the photograph is not clear), but meiosis is sometimes irregular, with a few sporangia producing aberrant spores. It may be an allotetraploid, probably derived from *W. polystichoides* and *W. ilvensis*.

9. *W. elongata* Hook. A medium-sized fern distributed in the Himalaya and SW China. Type from Sikkim, Himalaya. The chromosome number has been reported as $n = 41$, diploid, by Mehra and Singh (1955). Material collected in Yunnan has been found to be tetraploid, $n = 82$ (Figure 10). Comparison of this material with Mehra's voucher has not been made.

10. *Protowoodsia manchuriensis* (Hook.) Ching Widely distributed in E Asia. Type from NE China. Kurita (1965) found $n = 33$ (diploid) in Japanese material; that from Liaoning is tetraploid with $n = 66$ (Figure 9).

11. *Cheilanthes indusiosa* (Christ) Ching A medium-sized fern found only in Yunnan. Type from Dali, W Yunnan. 74 bivalents are formed at diakinesis (Figure 11), but these are often divided into two groups of 41 and 33 bivalents in each SMC. This is a common phenomenon in the SMCs (Figure 12). In a few sporangia meiosis is irregular, and aberrant spores can be found. It may be an allopolyploid, possibly the bigeneric hybrid between *Protowoodsia manchuriensis* and *Woodsia elongata*, from cytological and morphological analysis. Further experimental study is needed.

DISCUSSION

Ching (1940) established the genus *Protowoodsia* based on *Woodsia manchuriensis*. Now it has been confirmed that its chromosome numbers, $n = 33$ and 66, are different from species of *Woodsia* ($n = 41$, 39 and 38 and their multiples). Morphologically there are differences, for example the sori of *Protowoodsia* are near the vein endings, and in *Woodsia* are situated at mid-vein; the perispore of *P. manchuriensis* is finely reticulate, unlike *Woodsia*.

The chromosome number of *Cheilanthes indusiosa*, $n = 74$, is different from the other two genera. This seems to support Ching's system (1978), where *Protowoodsia* and *Cheilanthes* are treated as two distinct genera. Morphologically, *Cheilanthes* is separated by a distinct plate-like indusium, that has a few lobes that vary in size and shape, though it seems to be related to *W. elongata* in having similar false marginal indusia.

TABLE 1. Chromosome numbers for 10 Chinese species of Woodsiaceae

Name	Locality	Chromosome numbers	Spore numbers	Ploidy	Figure	Voucher specimens* **
1. * <i>Woodsia lanosa</i> Hook.	Cangshan Yunnan	n=164	64	8x	1	83
2. * <i>Wandersonii</i> (Bedd.) Christ	Cangshan Yunnan	n=164	64	8x	2	82
3. * <i>W.rosthorniana</i> Diels	Cangshan Yunnan	n=82	64	4x	3	2103
4. * <i>W.cycloloba</i> Hand-maz.	Muli Sichuan	n=164	64	8x	4	12376
5. <i>W.ilvensis</i> R.Br.	Mishan Heilongjiang	n=39	64	2x	5	103
6. <i>W.polystichoides</i> Eat. var. <i>polystichoides</i>	Fenghuangshan Liaoning	n=41	64	2x	6	205
7. * <i>W.polystichoides</i> Eat. var. <i>sinuata</i> Hook.	Fenghuangshan Liaoning	n=41	64	2x	7	207
8. * <i>W.subcordata</i> Turcz.	Fenghuangshan Liaoning	n=c. 80	64	4x	8	203
9. * <i>W.elongata</i> Hook.	Jizushan Yunnan	n=82	64	4x	10	1651
10. * <i>Protowoodsia manchuriensis</i> (Hook.) Ching	Fenghuangshan Liaoning	n=66	64	4x	9	202
11. * <i>Cheilanthesis indusiosa</i> (Christ) Ching	Jizushan Yunnan	n=74	64	4x	11, 12	157

* first report

** Collected by Mr. Q. Xia & Y. L. Ma and determined by Prof. R. C. Ching.

Intragenetic sub-divisions of *Woodsia* have differed with different authors. Tagawa (1937) divided the genus into four Sections: *Euwoodsia* Hook., *Eriosorus* Ching, *Perrinia* Hook. and *Physematium* Hook. He put stress on the presence of articulation on the petiole and morphology of the indusium. No cytological data were available at this time. Now chromosome numbers of over 20 species have been confirmed (Table 2). With the data available from both cytology and morphology, it is suggested that *Woodsia* be divided into five Sections (Table 3): *Eriosorus*, *Woodsia*, *Acrolysis*, *Physematium* and *Perrinia*. Within each Section there is one basic chromosome number, with the exception of *Woodsia* and possibly *Perrinia*. Some key morphological characters correspond with these Sections, for example in Sect. *Woodsia* (mostly $x = 39$) the articulation on the petiole is below the attachment of the first pair of pinnae, while in Sect. *Acrolysis* ($x = 41$) the articulation is at the position of the attachment of the first pair of pinnae.

There has been much debate among authors concerning the phylogeny of Woodsiaceae. Bower (1928, 1935) considered that *Woodsia* is derived from Cyatheaceae whose phylogenetic origin could be sought in Gleicheniaceae. Ching (1940) also favoured a Cyatheaceae-Woodsiaceae series. Pichi Sermolli (1959) suggested that Cyatheales originated in the ancestors of modern Gleicheniales, and that Aspidiales including Woodsioideae also originated in Gleichenioid ancestors. From cytological data, Mehra (1961) disagreed with Bower's view; he thought that Woodsiaceae ($x = 41$) could not directly be derived from Cyatheaceae ($x = 69, 70$). Reviewing these theories, Kurita (1965) considered that $n = 33$ and 39 in *Woodsia* suggested affinities with $n = 34$ and 39 in Gleicheniaceae.

The basic number in the most primitive group in *Woodsia*, Sect. *Eriosorus*, is $x = 41$. The basic chromosome numbers in *Woodsia* form a series from $x = 41$, with aneuploid reduction to $x = 39$ and 38. The author considers that $x = 41, 39$ and 38 in *Woodsia* may be related to $n = 43$ in *Dicranopteris*, and that $x = 33$ in *Protowoodsia* may be related to $n = 34$ in *Sticherus*. *Cheilanthesis* may have originated from hybridization between *Woodsia* and *Protowoodsia*. Woodsiaceae may be derived from the common ancestor of modern *Dicranopteris* and *Sticherus*.

TABLE 2. Chromosome numbers for all species of Woodsiaceae

Taxon	Chromosome numbers	Authority
<i>Woodsia</i> R.Br.	x=41, 39, 38	
Sect. <i>Eriosorus</i> Ching	x=41	
<i>W. macrospora</i> C. Chr. et Maxon	no information	
<i>W. cinnamomea</i> Christ	no information	
<i>W. lanosa</i> Hook.	n=164	Y. L. Ma (present paper)
<i>W. rosthorniana</i> Diels	n=82	Y. L. Ma (present paper)
<i>W. andersonii</i> (Bedd.) Christ	n=164	Y. L. Ma (present paper)
<i>W. cycloloba</i> Hand-Maz.	n=164	Y. L. Ma (present paper)
Sec. <i>Woodsia</i>	x=39	
<i>W. shensiensis</i> Ching	no information	
<i>W. pulchella</i> Bertol	n=39 2n=78	Meyer (1959)
<i>W. glabella</i> R.Br.	n=39 2n=78	Britton (in Fabbri 1963) (1964) Love, A. (1970) Love & Love (1976)
<i>W. hancockii</i> Bak.	no information	
<i>W. ilvensis</i> R.Br.	n=c41	Manton (1950)
	n=40-41	Britton (1953) Taylor & Lang (1963)
	n=41 2n=82	Love & Love (1961) Sorsa (1961, 1962) Vida (1965)
	n=39 2n=78	Love & Love (1976) Y. L. Ma (present paper)
<i>W. alpina</i> Gray. ssp. <i>alpina</i>	n=82	Love & Love (1961) Vida (1965)
	n=78 2n=156	Love & Love (1976)
<i>W. alpina</i> Gray. ssp. <i>belli</i> (Lawson) Love & Love	n=78 2n=156	Love & Love (1976)
Sect. <i>Acrolysis</i> (Nakai) Y. L. Ma comb. nov.	n=41	
<i>W. macrochleana</i> Mett.	n=41 2n=82	Kurita (1965) Mitui (1966, 1968)
<i>W. oblonga</i> Ching et S. H. Wu	no information	
<i>W. pilosa</i> Ching	no information	
<i>W. intermedia</i> Tagawa	n=82 2n=164	Shimura & Matsumoto (1975)
<i>W. polystichoides</i> Eat. var. <i>polystichoides</i>	n=41 2n=82	Kurita (1961) Mitui (1968) Hirabayashi (1969) Tatuno & Okado (1970) Y. L. Ma (present paper)
<i>W. polystichoides</i> Eat. var. <i>sinuata</i> Hook.	n=41	Y. L. Ma (present paper)
<i>W. subcordata</i> Turcz.	n=c. 80	Y. L. Ma. (present paper)
Sect. <i>Physematium</i> (Kif.) Hook. emend.	x=41	
<i>W. elongata</i> Hook.	n=41	Mehra & Singh (1955)
	n=82	Y. L. Ma (present paper)
Sect. <i>Perrinia</i> Hook.	x=38	
<i>W. scopulina</i> Eat. var. <i>scopulina</i>	n=38 2n=76	Wagner (in Fabbri 1963) Brown (1964) Taylor & Brockman (1966)
	n=38 2n=76	Brown (1964)
<i>W. scopulina</i> Eat. var. <i>appalachiana</i> (Taylor) Morton	n=38 2n=76	Brown (1964)
<i>W. montevidensis</i> (Spreng.) Hieron.	no information	
<i>W. oregana</i> Eat.	n=38 2n=76	Brown (1964)
<i>W. cathcartiana</i> Robins.	n=76 2n=152	Brown (1964)
<i>W. obtusa</i> (Spreng.) Terr.	n=76 2n=152	Brown (1964) Wagner & Wagner (1966)
	n=78 2n=156	Wagner, Farrar & McAlpin (1970)

TABLE 2 (continued)

<i>W. plummerae</i> Lemmon	n=76 2n=152	Smith, A.R. (1974)
<i>W. mexicana</i> Fee	n=c. 76 2n=c. 152	Brown (1964)
	n=82 2n=164	Knobloch & Correll (1962)
<i>Protowoodsia</i> Ching	x=33	
<i>P. manchuriensis</i> (Hook.) Ching	n=33 2n=66	Kurita (1965) Mitui (1965, 1966, 1968)
	n=66	Y. L. Ma (present paper)
<i>Cheilanthesopsis</i> Hieron.	x=74?	
<i>C. indusiosa</i> (Christ) Ching	n=74	Y. L. Ma (present paper)
* <i>W. mollis</i> (Klf.) J. Smith	no information	
* <i>W. fragilis</i> (Trev.) Moore	no information	

*Species incertae sedis.

TABLE 3. Key to Sections of *Woodsia*

1. Needle-pointed articulate hairs; petiole with or without articulation
 2. Petiole without articulation; $x = 41$, Sect. *Eriosorus* Ching in Sinensia 3: 134. 1932. Lectotypus *W. lanosa* Hook.
 2. Petiole jointed
 3. Petiole jointed below the attachment of the first pair of pinnae; $x = 39$ (41) Sect. *Woodsia* — based on Subsect. *Ilvensis* Ching. 1.c.
 3. Petiole jointed at the position of attachment of the first pair of pinnae; $x = 41$, Sect. *Acrolysis* (Nakai) Y. L. Ma comb. nov. — based on Subsect. *Acrolysis* Nakai in Bot. Tokyo 39: 76. 1925. Lectotypus *Woodsia polystichoides* Eat.
1. Cylindrical or capitate hairs; petiole not jointed
 2. Presence of reflexed false indusia in addition to true indusia; $x = 41$, Sect. *Physematium* (Klf.) Hook. Sp. Fil. vol. 1. 1844. Lectotypus *W. elongata* Hook.
 2. No false indusia, the indusium with deeply lacinate separated lobes, hidden under the sori; $x = 38^*$, Sect. *Perrinia* Hook. 1.c. Lectotypus *W. scopulina* Eat.

*The chromosome numbers $n = 78$ in *W. obtusa* (Wagner, Farrar & McAlpin 1970) and $n = 82$ in *W. mexicana* (Knobloch & Correll 1962) have been reported but do not correspond with $n = 76$ for these two species recorded by many other authors (see Table 2).

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ECOLOGICAL OBSERVATIONS ON THE PTERIDOPHYTE FLORA OF LANGTANG NATIONAL PARK, CENTRAL NEPAL

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ABSTRACT

An ecological account of the pteridophyte flora of Langtang National Park of central Nepal is given, based on plants collected during botanical tours made during 1977-1979. 142 species of ferns and 11 species of fern-allies in 47 genera inhabiting tropical to alpine regions (1230 - 4420m altitude) are reported and related to habitats with ecological and altitudinal data.

INTRODUCTION

Langtang National Park is situated in the central Himalayan region of Nepal to the north of Kathmandu (see Figure 1). The area is particularly rich in ferns. Relatively little attention has hitherto been given to the species of this region, and publications on its flora are meagre. The present report is based on botanical tours made in this area during 1977-1979.

GEOGRAPHY OF THE REGION

The area under study is from Manigaon to Langtang-Gosainkund and Helambu (parts of Rasuwa and Sindhupalchok districts respectively) which lie within the Park (28° to $28^{\circ}20'N$ latitude and $85^{\circ}15'$ to $86^{\circ}E$ longitude in the inner Himalayan ranges, 1230-4420m). From this area, extensive collections of tropical to alpine ferns and fern-allies have been made over an area of about 480 sq. miles.

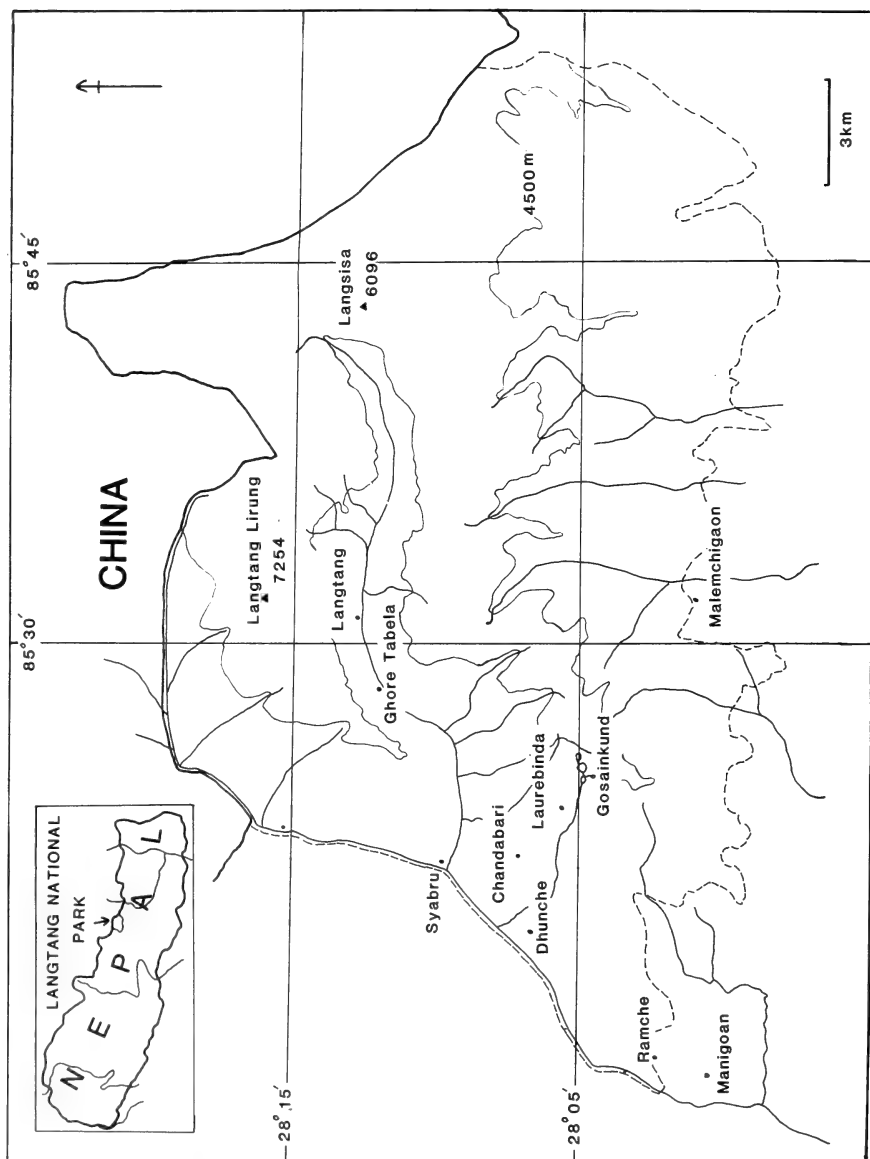
The area of the Langtang valley is of considerable scenic beauty, consisting of alpine meadows, lakes, glacial rivulets and the Himalayan Peaks of Langsisa (6096m) and Langtang Lirung (7245m). The sacred lake of Gosainkund (4420m) is the place from where Wallich, in 1820, procured some of the earliest gatherings of alpine plants made in the Himalaya.

The character of the Langtang National Park varies from one of cool summers in the valley to a tundra type of climate on the peaks of the Himalayan range. Temperatures throughout the region also vary widely with aspect, altitude and cloud cover, and are generally highest from May to July and lowest from December to February. Precipitation in the region varies not only with altitude, but also widely through the year (see Table 1). The monsoon occurs between June and September, varying locally with topography and altitude. The area of lower valley, which receives quite heavy rainfall annually, also remains enveloped in thick clouds during the principal rainy months of June to September, when it rains almost daily and the humidity is at a maximum. In the upper valley, heavy downpours are generally less frequent.

TABLE 1. Precipitation summary for 4 stations in Langtang National Park for the years 1976-1980 (from data kindly supplied by the meteorological service of His Majesty's Government of Nepal)

	DHUNCHE	TARKEGHYANG	SHARMATHANG	TIMURE
Lowest minimum	6mm (Nov-Dec 1975)	1mm (Nov. 1978)	3mm (Nov. 1976)	1mm (Jan 1977)
Highest maximum	649mm (Aug. 1975)	763mm (July 1978)	1524mm (July 1978)	301mm (July 1978)
Lowest annual amount	1661mm (1977)	772mm (1975)	3576mm (1976)	252mm (1976)
Highest annual amount	2433mm (1979)	2668mm (1978)	4975mm (1978)	1123mm (1978)
Maximum in 24 hrs.	100mm (8 June 1976)	96mm (2 June 1978)	142mm (24 July 1979)	69mm (13 Sept. 1977)

FIGURE 1. Map of Langtang National Park.



The soil of the hills and mountains in the upper valley above 3000m is composed mainly of sandy loam with a large proportion of gravels. In the lower forested region (2000 - 3000m) there is a covering humus layer of 2 - 10cm depth. This serves as a good substratum for the growth of terrestrial species. Below 1000m there are also red and yellow clays.

GENERAL VEGETATION

On the way to Langtang National Park the following forest types have been observed. At the lowest elevations (up to 1000m) the area carries a tropical Low Hill Forest, dominated by trees of *Shorea robusta*. Between the area of Manigaon to Dhunche (1230-2000m) most of the mountain slopes have been cleared of forest for cultivation and a number of encroachment areas are observed. Consequently only a few thick forests are seen, representing the original sub-tropical Middle Hill Forest. *Pinus roxburghii*, *Schima wallichii*, *Castanopsis indica*, *C. tribuloides* and *Lyonia* are the most striking trees of the forest. Between the area of Khangjing and Ghore Tabela (2000 - 3000m) elevation, is temperate Upper Hill Forest. This is a damp and dark ever-green Oak and mixed broadleaved forest composed of *Quercus semecarpifolia*, *Q. lanuginosa*, *Q. glauca*, *Q. lamellosa*, *Q. incana*, *Pinus wallichiana* and *Tsuga dumosa*. To the east of the gorge of Trisuli River are *Tsuga* covered hills. With increasing altitude, *Rhododendron arboreum*, *R. campanulatum* and *Alnus nepalensis* occur luxuriantly and the forest becomes gloomier. The Oaks here bear branched crowns and are profusely covered with mosses and epiphytic ferns. The forest is thick and moist. The shelter of the trees provides shade and helps to prevent rapid air movements to a considerable extent, resulting in a prolific growth of small herbs, shrubs and ferns on the forest floor. Higher up there is gradual replacement of Oaks by *Rhododendron*, marking the beginning of the sub-alpine *Rhododendron*-Conifer Zone. In the area from Ghore Tabela to Langtang village (3000 - 4000m) on the north-facing mountain slopes is preserved a very rich collection of conifers in a forest composed mainly of *Abies spectabilis*, *Betula utilis* and *Rhododendron arboreum* var. *cambellii*. The Himalayan Silver Fir, *Abies spectabilis*, forest is locally a very striking feature, from Chandabari and Laurebinda. The south-facing mountain slopes are partly grass-covered, but also have *Larix himalaica*, dwarf bushes of *Rhododendron lepidotum*, *Juniperus recurva*, *Allium wallichii*, *Ephedra jerardiana*, *Rosa macrophylla*, *Caragana* sp. and scrub of *Cotoniaster*. *Betula utilis* is found in the high level *Rhododendron* forest of the southern mountain range of the upper Langtang valley. At heights above 4000m on exposed sunny slopes there is often a mosaic of *Rhododendron campanulatum* or scrub of *Rhododendron lepidotum*, *R. anthopogon* and *Caragana* sp. with *Aconitum* beneath. Grass-lands are also frequent in this area or above, giving way eventually to rocky moraine with scattered grasses and herbs.

EPIPHYTIC FERNS

The composition of the epiphytic element changes markedly with altitude as well as the shady or exposed nature of the forest. Certain species like *Shorea robusta* in the lower hill forest and the conifers at higher elevations do not afford shelter for many epiphytic ferns.

Due to the relative high temperature and low humidity the epiphytes of the low hill zone (up to 1000m) have developed marked features for storing water. Common species on *Shorea robusta* are *Lepisorus nudus* and *Pyrrosia mollis*, in which the fronds roll inwards from their margins to conserve water during dry weather.

Epiphytic ferns in the middle hill zone (1000 - 2000m) are mostly influenced by the monsoon. During this season they appear prolifically, complete their annual cycle and their fronds wither. The rhizomes remain dormant to renew their activity the following year. Due to the prevailing warm temperature, adequate rainfall and high humidity, the branches and trunks of trees are often thickly covered with mosses and liverworts which serve as a sponge for water absorption, helping protect the rhizomes of epiphytic ferns from drought. The common epiphytes growing mainly on *Schima wallichii* and *Castanopsis indica* in rather open sites are *Asplenium laciniatum*,

Arthromeris wallichiana, *Drynaria mollis*, *Crypsinus hastatus*, *Polypodium lachnopus*, *Pyrrosia mollis* and *Oleandra wallichii*. *Oleandra wallichii* possesses a strongly branched rhizome which gives off stiff rhizome-like roots into the humus of the tree trunks. In more shaded areas of trunks of *Castanopsis indica*, *C. tribuloides* or *Lyonia* sp. are *Asplenium ensiforme*, *Lepisorus nudus*, *L. kashyapii*, *Polypodium amaurolepidia*, *P. amoenum*, *P. argutum* and *P. microrhizoma*.

The Quercus-Rhododendron Zone (2000 - 3000m) also has favourable conditions for epiphytic growth. Some of the commonest species on the trunks of *Quercus semecarpifolia* and *Q. lanuginosa* in the more open parts of this area are *Davallodes membranulosum*, *Crypsinus ebenipes*, *Drynaria mollis*, *Lepisorus clathratus* and *L. kashyapii*. In shaded and more moist parts of the area, mostly on the trunks of *Quercus glauca*, *Q. lamellosa*, *Q. incana*, *Rhododendron arboreum*, *R. campanulatum* and *Alnus nepalensis*, there are *Araiostegia clarkei*, *A. delavayi*, *A. pulchra*, *Leucostegia immersa*, *Arthromeris himalayensis*, *Crypsinus oxylobus*, *C. quasidivariatus*, *Drynaria propinqua*, *Lepisorus loriformis*, *Polypodium argutum* and *Pyrrosia mollis*. Another conspicuous fern is *Vittaria flexuosa*, hanging from lower tree trunks.

In the Rhododendron-Conifer zone the epiphytic ferns decrease above 3000m. At the top of ridges the trees are rather short and stunted due to direct exposure to strong winds, but during the monsoon they receive plenty of rain and their branches are almost continuously immersed in fog. As a consequence they are thickly clothed with liverworts and mosses, forming a substrate for prolific growth of *Polypodium lachnopus* especially on *Rhododendron arboreum* var. *campbellii*. In shady areas *Araiostegia delavayi* and *Lepisorus kashyapii* are seen more frequently.

TERRESTRIAL FERNS

At lower elevations under 1000m the forest floor is fairly poor in humus and the soil is composed of reddish-brown clay. Here growing abundantly are *Adiantum caudatum*, *A. philippense*, *Onychium siliculosum*, *Pityrogramma calomelanos* and *Sphenomeris chinensis*. In partly shaded places *Tectaria macrodonta* and *Pteris dactylina* become predominant. *Pteris aspericaulis* and *Athyrium acrostichoides* frequently colonise the more open forest borders and *Equisetum debile* occurs on gravelly soil especially at waysides.

A vast number of ferns grow on the forest floor between 1000 - 2000m. The most frequent are *Diplazium multicaudatum*, *D. esculentum*, *Athyrium macrocarpum*, *A. pectinatum*, *Dryopteris atrata*, *D. cochleata*, *D. marginata*, *D. panda*, *Polystichum lentum*, *P. squarrosum*, *Thelypteris auriculata*, *T. extensa*, *T. ornata*, *T. paludosa*, *Botrychium lanuginosum*, *Mecodium exsertum*, *Woodwardia unigemmata* and *Arthromeris wallichiana*. On dry and exposed places along forest borders *Dennstaedtia appendiculata* often flourishes with *Polystichum prescottianum*, *Onychium lucidum*, *Lepisorus nudus*, *Microsorium membranaceum*, *Polypodium amoenum*, *Pyrrosia flocculosa*, *Vittaria flexuosa*, *Selaginella monospora*, *S. subdiaphana*, *Mecodium exsertum*, *Leucostegia delavayi*, *L. immersa* and *Nephrolepis cordifolia*.

At higher elevations, between 2000 - 3000m on the forest floor a large number of terrestrial ferns form an exuberant growth in the shade of trees and shrubs. The more common ferns are *Pteris aspericaulis*, *P. vittata*, *Acrophorus stipellatus*, *Athyrium macdonnellii*, *A. macrocarpum*, *Dryopteris paleacea*, *Thelypteris erubescens*, *Cheilanthes grisea*, *Coniogramme caudata* and *C. fraxinea*. The borders of the forest are covered with many plants of *Dennstaedtia appendiculata*, *Leucostegia immersa*, *Athyrium filix-femina*, *A. foliolosum*, *A. japonicum*, *A. setiferum*, *Diplazium stoliczkae*, *Dryopteris chrysocoma*, *D. marginata*, *D. odontoloma*, *Peranema cyatheoides*, *Pteris biaurita*, *P. cretica*, *P. excelsa*, *P. aspericaulis*, *Polystichum lentum*, *P.*

nigropaleaceum, *P. squarrosus*, *P. stimulans*, *Thelypteris arida*, *T. dentata*, *T. esquirolii*, *Woodwardia unigemmata*, *Asplenium ensiforme*, *A. indicum*, *Arthromeris himalayensis*, *Lepisorus loriformis*, *Microsorium membranaceum*, *Lycopodium hamiltonii*, *Selaginella chrysocaulos* and *S. subdiaphana*. A characteristic fern of the margins of this forest is *Pteris wallichiana*, which possesses a large digitately compound frond springing from an ascending rhizome. On moist gravelly soils or in damp places along waysides or water channels near the forest margins *Equisetum diffusum* grows in profusion.

The most significant undergrowths of *Quercus-Rhododendron* forest are formed by *Athyrium acrostichoides*, *A. macdonellii*, *A. macrocarpum* and *A. nigripes*. This community can cover a vast area of the forest floor between 2700 - 3100m.

On forest borders or in open places the *Athyrium* community is replaced by *Dennestaedtia appendiculata*, *Pteris cretica*, *P. quadriaurita*, *Araiostegia clarkei*, *Dryopteris brunoniana*, *D. chrysocoma*, *Diplazium multicaudatum*, *Polystichum nepalensis*, *P. nigropaleaceum*, and *Thelypteris paludosa*. On the higher limits of the *Quercus-Rhododendron* forest (3000 - 4000m) *Dryopteris brunoniana* and *Polystichum prescottianum* become prominent on the forest floor or along forest margins.

THICKET-FORMING SPECIES

At elevations of up to 2000m *Dicranopteris linearis* is a characteristic species on exposed ridges of ravines, open rocky hills and on gravelly soil along waysides. It is exposed to wide variations of temperature and is able to tolerate direct sun as well as moist cool winds. It is a good soil binder as it forms thickets, but it seems to exclude all other species from growing in the area it occupies. *Gleichenia glauca* forms extensive thickets between 2000 - 3000m. The young fronds bear a pair of opposite pinnae while the apex becomes dormant and is closely surrounded by scales. In the following year another pair of pinnae is formed by the activation of the terminal bud of the frond, after which it becomes dormant again. This process is repeated year after year until the fronds reach huge dimensions. *Pteridium aquilinum* occurs extensively over the area, forming huge dark green thickets in open places between 1230 - 3400m. The fronds are large and the rhizomes deep underground. It is one of the species that sprouts vigorously after burning. Thus these tough ferns play a useful role in reducing soil erosion and landslides.

CLIMBERS

Most climbers are in the lower zones; for example *Lygodium flexuosum* and *L. japonicum* are fairly common in the open areas as well as on the forest floor between about 1230 - 1900m. They grow on humus rich soil and the rachides of the fronds twine around neighbouring shrubs or branches of trees, enabling them to climb to great heights and into bright lights conditions.

RAVINE FERNS

This category includes all the fern species which grow in ravines along water channels on calcareous stony soil. At lower altitudes, to about 1000m, *Ceratopteris thalictroides* occurs scattered along sandy or clayey edges of water channels. On moist rocks along the streams at higher elevations (2000 - 3000m), are found *Dryopteris marginata*, *Polystichum aculeatum*, *Thelypteris auriculata*, *Asplenium ensiforme*, *Drynaria propinqua*, *Lepisorus kashyapii*, *Microsorium membranaceum*, *Crypsinus malacodon* and *Polypodium lachnopus*. *Lycopodium clavatum* also grows near water courses with *Equisetum debile*.

LITHOPHYTES

True rock ferns

The species that colonise dry boulders and rock crevices at low altitudes (1000m) include *Cheilanthes dalhousiae*, *C. albomarginata*, *C. tenuifolia*, *Pityrogramma calomelanos*, *Onychium siliculosum*, *Adiantum philippense* and *Sphenomeris chinensis*. Between 1000 - 2000m the more common species are *Pteris aspericaulis*, *P. wallichiana*, *Araiostegia pulchra*, *Davallodes membranulosum*, *Athyrium drepanopterum*, *Dennstaedtia appendiculata*, *Mecodium crispatum*, *Diplazium giganteum*, *Hypodematium crenatum*, *Asplenium laciniatum*, *Arthromeris himalayensis* and *A. wallichiana*, and associations of these species can be particularly abundant. Less frequent are *Crypsinus oxylobus*, *Drynaria propinqua*, *Loxogramme involuta*, *Microsorium cuspidatum*, *M. membranaceum*, *Lycopodium hamiltonii* and *L. ulicifolium*.

Growing luxuriantly on shady and moist rocks within the forest between 2000 - 3000m altitude are *Adiantum venustum*, *Cheilanthes anceps*, *Dryopteris odontoloma*, *Polystichum aculeatum*, *P. neolobatum*, *P. obliquum*, *P. squarrosus* and *P. stimulans*. Occasionally large plants of *Woodwardia unigemmata* occur here, and large species of *Asplenium* including *A. ensiforme*, *A. laciniatum* and *A. varians*.

Many epiphytes also grow as rock ferns on moist, shady rocks within the forest because of the mild, moist, humid conditions. The dominant species are *Crypsinus oxylobus*, *Drynaria mollis*, *D. propinqua*, *Lepisorus nudus*, *L. scolopendrium*, *Crypsinus hastatus*, *Polypodium amoenum*, *P. lachnopus* and *Vittaria flexuosa*. Less frequent are *Selaginella involvens*, *S. pennata*, *S. subdiaphana*, *Dryopteris concolor* and *Adiantum venustum*, especially on dry exposed rocks along waysides.

Between 3000 and 4000m *Woodsia elongata* luxuriantly colonises exposed dry rocks. Other abundant species are *Cheilanthes albomarginata*, *C. dalhousiae*, *C. subvillosa*, *Cryptogramma crispa*, *Polystichum atkinsonii*, *P. prescottianum*, *Thelypteris elwesii*, *Lepisorus kashyapii*, *Crypsinus malacodon*, *Dryopteris chrysocoma* and *Pteridium aquilinum*.

Above 4000m *Dryopteris brunoniana* and *Polystichum prescottianum* appear.

Ferns of stone-wall crevices and gravel embankments

The main xerophytic ferns that thrive well in these dry and exposed habitats between 1000 - 2000m are *Pteris biaurita*, *P. vittata*, *Thelypteris torresiana* and *Tectaria macrodonta*, whilst *Nephrolepis cordifolia* may cover enormous areas locally. This last species possesses thin, wiry, widely creeping, branched runners which sprout at intervals to give rise to new individuals. The branches of these runners bear whitish edible water tubers at their ends. Under extremely dry conditions the fronds shed their pinnae whilst the rachides persist. Less abundant species are *Osmunda claytoniana*, *Pteris nepalensis*, *Leucostegia immersa*, *Hypodematium crenatum*, *Thelypteris molliuscula*, *Microsorium membranaceum*, *Polypodium lachnopus*, *Lycopodium clavatum* and *Selaginella involvens*.

At the higher elevations (2000 - 3000m) the number of ferns diminishes in this habitat, but *Botrychium lanuginosum*, *Dryopteris chrysocoma*, *Dennstaedtia appendiculata* and *Oleandra wallichii* can be found. Above 3000m, only *Crypsinus ebenipes* and *Cryptogramma brunoniana* are frequent, but above 4000m elevation only *Cryptogramma brunoniana* is present.

PHYTOGEOGRAPHICAL COMPARISON

The pteridophyte flora of Langtang National Park, central Nepal resembles both the east and west Nepal floras (see Table 2). Analysis of the distribution of the species in Nepal is as follows:—

a. No. of species from Langtang National Park, central Nepal	153
b. No. of species common with east Nepal	125 (81.69%)
c. No. of species common with west Nepal	60 (39.21%)
d. No. of species found only in Langtang National Park	19 (12.41%)

The above comparison shows that the pteridophyte flora of Langtang National Park has affinities with the floras of both east and west Nepal, although there are more species in common with those of east Nepal (81.69%), than with those of west Nepal (39.21%).

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TABLE 2. Phytogeographical distribution of ferns in Nepal Himalaya in relation to Langtang National Park region.

Key to distributions:

- 1 West Nepal (the area lying on 80° to 83°E longitude).
- 2 Central Nepal (the area lying on 85°15' to 86°E longitude).
- 3 East Nepal (the area lying on 86°30' to 88°10'E longitude).

Scientific name	Distribution	Scientific name	Distribution
<i>Botrychium lanuginosum</i>	1 2	<i>C. affinis</i>	1 2 3
<i>Osmunda claytoniana</i>	1 2 3	<i>C. fraxinea</i>	2 3
<i>Lygodium flexuosum</i>	1 2 3	<i>Cryptogramma crispa</i>	1 2 3
<i>L. japonicum</i>	2 3	<i>Dennstaedtia appendiculata</i>	2 3
<i>Dicranopteris linearis</i>	2 3	<i>Doryopteris concolor</i>	2 3
<i>Gleichenia glauca</i>	2 3	<i>Onychium contiguum</i>	1 2 3
<i>Mecodium badium</i>	1 2 3	<i>O. japonicum</i>	2 3
<i>M. crispatum</i>	1 2 3	<i>O. lucidum</i>	2
<i>M. exsertum</i>	2 3	<i>O. siliculosum</i>	2 3
<i>Actiniopteris semiflabellata</i>	2 3	<i>Pityrogramma calomelanos</i>	2 3
<i>Adiantum caudatum</i>	2 3	<i>Pteridium aquilinum</i>	1 2 3
<i>A. edgeworthii</i>	1 2	<i>Pteris aspericaulis</i>	2 3
<i>A. philippense</i>	1 2 3	<i>P. biaurita</i>	1 2 3
<i>A. venustum</i>	1 2	<i>P. cretica</i>	1 2 3
<i>Cheilanthes anceps</i>	2 3	<i>P. dactylina</i>	1 2 3
<i>C. albomarginata</i>	1 2 3	<i>P. excelsa</i>	1 2 3
<i>C. dalhousiae</i>	1 2 3	<i>P. geminata</i>	1 2
<i>C. farinosa</i>	1 2 3	<i>P. nepalensis</i>	2 3
<i>C. grisea</i>	2	<i>P. quadriaurita</i>	1 2 3
<i>C. rufa</i>	1 2 3	<i>P. vittata</i>	1 2 3
<i>C. subvillosa</i>	2	<i>P. wallichiana</i>	1 2 3
<i>C. tenuifolia</i>	2 3	<i>Sphenomeris chinensis</i>	2 3
<i>Coniogramme caudata</i>	2 3	<i>Ceratopteris thalictroides</i>	1 2

Scientific name	Distribution	Scientific name	Distribution
<i>Araiostegia clarkei</i>	2	<i>T. erubescens</i>	2 3
<i>A. dareiformis</i>	2 3	<i>T. esquirolii</i>	2
<i>A. delavayi</i>	2 3	<i>T. extensa</i>	2
<i>A. pulchra</i>	1 2 3	<i>T. molliuscula</i>	2 3
<i>Davallodes membranulosum</i>	2 3	<i>T. ornata</i>	2 3
<i>Leucostegia immersa</i>	1 2 3	<i>T. paludosa</i>	2 3
<i>Nephrolepis cordifolia</i>	2 3	<i>T. torresiana</i>	2 3
<i>Oleandra wallichii</i>	1 2 3	<i>Woodsia elongata</i>	1 2
<i>Acrophorus stipellatus</i>	2 3	<i>Woodwardia unigemmata</i>	1 2 3
<i>Athyrium acrostichoides</i>	2	<i>Asplenium ensiforme</i>	1 2 3
<i>A. drepanopterum</i>	2 3	<i>A. indicum</i>	2 3
<i>A. filix-femina</i>	1 2 3	<i>A. laciniatum</i>	2 3
<i>A. foliolosum</i>	1 2	<i>A. unilaterale</i>	2 3
<i>A. macdonnellii</i>	2 3	<i>A. varians</i>	1 2 3
<i>A. macrocarpum</i>	2 3	<i>Arthromeris himalayensis</i>	2 3
<i>A. nigripes</i>	2 3	<i>A. wallichiana</i>	1 2 3
<i>A. pectinatum</i>	2 3	<i>Crypsinus ebenipes</i>	2 3
<i>A. setiferum</i>	2 3	<i>C. oxylobus</i>	2 3
<i>A. tenellum</i>	2	<i>C. quasidivaricatus</i>	2 3
<i>Diplazium esculentum</i>	1 2 3	<i>Drynaria mollis</i>	2 3
<i>D. giganteum</i>	2	<i>D. propinqua</i>	1 2 3
<i>D. multicaudatum</i>	2	<i>Lepisorus clathratus</i>	2 3
<i>D. stoliczkae</i>	1 2 3	<i>L. excavatus</i>	2
<i>Dryopteris acutodentata</i>	2 3	<i>L. kashyapii</i>	2 3
<i>D. apiciflora</i>	1 2	<i>L. loriformis</i>	1 2 3
<i>D. atrata</i>	1 2 3	<i>L. nudus</i>	1 2 3
<i>D. barbigera</i>	1 2 3	<i>L. scolopendrium</i>	2 3
<i>D. brunoniana</i>	1 2 3	<i>Loxogramme involuta</i>	1 2 3
<i>D. chrysocoma</i>	1 2 3	<i>Microsorium cuspidatum</i>	2 3
<i>D. cochleata</i>	2 3	<i>M. membranaceum</i>	2 3
<i>D. marginata</i>	2 3	<i>Crypsinus hastatus</i>	2
<i>D. odontoloma</i>	2 3	<i>C. malacodon</i>	1 2 3
<i>D. paleacea</i>	2 3	<i>Polypodium amaurolepida</i>	2
<i>D. panda</i>	2 3	<i>P. amoenum</i>	2 3
<i>D. sinofibrillosa</i>	2 3	<i>P. argutum</i>	1 2 3
<i>Elaphoglossum petiolatum</i>	2 3	<i>P. atkinsonii</i>	2 3
<i>Hypodematum crenatum</i>	2	<i>P. lachnopus</i>	1 2 3
<i>Peranema cyatheoides</i>	2 3	<i>P. microrrhizoma</i>	1 2 3
<i>Polystichum aculeatum</i>	2	<i>Pyrrosia flocculosa</i>	1 2 3
<i>P. atkinsonii</i>	2 3	<i>P. mollis</i>	1 2 3
<i>P. lentum</i>	1 2 3	<i>Vittaria flexuosa</i>	2 3
<i>P. neolobatum</i>	2 3	<i>Lycopodium clavatum</i>	2 3
<i>P. nepalense</i>	2 3	<i>L. hamiltonii</i>	2
<i>P. nigropaleaceum</i>	2 3	<i>L. ulicifolium</i>	2
<i>P. obliquum</i>	1 2	<i>Selaginella chrysocaulos</i>	2 3
<i>P. prescottianum</i>	1 2 3	<i>S. involvens</i>	2 3
<i>P. squarrosus</i>	1 2 3	<i>S. monospora</i>	2 3
<i>P. setiferum</i>	2 3	<i>S. pennata</i>	2 3
<i>P. stimulans</i>	1 2 3	<i>S. subdiaphana</i>	2 3
<i>Tectaria coadunata</i>	2	<i>S. vaginata</i>	2 3
<i>T. macrodonta</i>	1 2 3	<i>Equisetum debile</i>	1 2 3
<i>Thelypteris arida</i>	1 2 3	<i>E. diffusum</i>	2 3
<i>T. auriculata</i>	2 3		
<i>T. dentata</i>	2 3		
<i>T. elwesii</i>	2		

NISTARIKA, A NEW GENUS OF POLYPODIACEAE FROM SILENT VALLEY, SOUTH INDIA

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ABSTRACT

A new genus, *Nistarika*, with one species, *N. bahupunctika*, is described, characterised by having four rows of simple fronds restricted to the dorsal surface of the rhizome, and lamina-less fertile fronds bearing sporangia directly on the midrib in two lateral linear sori. The genus is related to *Leptochilus* (Polypodiaceae) and is possibly derived from *Microsorium*.

INTRODUCTION

Silent Valley, a small, rather densely forested area of the Western Ghats of south India close to the Palghat Saddle on the western fringe of Nilagiri ranges, has recently attracted attention as one of the few undisturbed wet evergreen tropical forests left in the Indian subcontinent. It is a small table-land on the western slope of Western Ghats, criss-crossed by many fast flowing rivulets which have cut deep into the terrain making it highly dissected. The slopes are covered by dense wet evergreen forests and in many cases the ridge crests are covered in grassland. Undergrowth is sparse in the wooded regions, except on the banks of streams and borders of grassland and other open areas. The climate is equatorial with a temperature range of 15-25°C, and an annual rainfall of c. 380cm, mostly from May to September. Even during the dry season (January-May) the forest floor never becomes exposed. As Silent Valley was botanically unexplored on account of its inaccessibility and the rugged terrain, a floristic study was undertaken of the fern flora and over 100 taxa recorded from the c. 2000ha studied (Nayar 1982). One of the ferns collected appears to be as yet unnamed; it is described here together with some aspects of its morphology. It grows in dense shade at forest margins and is fairly widespread in the Panthanthodu and Kummattanthodu areas but is less abundant on the banks of Kunthippuzha River in the southern half of Silent Valley Reserve forest.

TAXONOMIC DESCRIPTION

Nistarika Nayar, Madhusoodanan & Molly genus novum

Genus *Leptochilo* simillimum, sed et foliis tri- vel quinquefariis in rhizomate dorsaliter dispositis et foliis fertilibus omnino sine lamina, sporangia vero nuda in costa gerentibus differt. Sorus linearis, exindusiatus, utroque costae latere continuus. Sporae monoletae, non perinatae.

Typus: *Nistarika bahupunctika* Nayar, Madhusoodanan & Molly.

A genus similar to *Leptochilus* but differing from it in having four rows of fronds restricted to the dorsal surface of the rhizome and in having the fertile frond totally devoid of any lamina but bearing sporangia directly on the midrib. Sorus linear, exindusiate and forming a lateral continuous line on either side of the midrib.

Nistarika bahupunctika Nayar, Madhusoodanan & Molly sp. nov.

Rhizoma ascendens, semi-epiphyticum, longum, sparse ramosum, plus minusve dorsiventraliter compressum, 5 - 8mm latum, 3 - 4mm crassum, viride, praeter ad apicem fere glabrum, dictyostelen faciens, sclerenchymate tenui fusoque in parenchymate dense disperso. Paleae parvae, peltatae, clathratae, glandibus ad apicem et basi pilis duobus glanduliferis conspicuisque praeditae. Folia tri- vel quinquefaria dorsaliter in rhizomate irregulatim disposita, dimorpha, simplicia. Folia sterilia patentia, stipitata, lamina herbacea, angusto-lanceolata 30 - 50cm longa (1.5) - 2.5 - 4cm lata, in apicem acuminatum gradatim contracta, margine integro, venatione reticulata. Folia fertilia erecta, filiformia, sine lamina, 45 - 75cm longa 1.5mm lata. Sorus exindusiatus, linearis, continuus utroque costae nuda latere. Sporae monoletae, c. 35 x 65µm, spinulosae, non perinatae.

Holotypus: CU 29263, lectus ab K.K. Geeverghese et B.K. Nayar in 28.3.1980 apud Panthenrhode, Silent Valley, India Meridionalis, et positus apud Central National Herbarium, Calcutta.

Isotypus: positus apud Herbarium Universitatis de Calicut.

Paratypi: positus apud Herbarium Universitatis de Calicut; CU 21329, lectus ab B.K. Nayar in 19.12.1977 et CU 29136 lectus ab B.K. Nayar et P.V. Madhusoodanan in 13.2.1980 apud Silent Valley.

Rhizome climbing vertically up supports and becoming semiepiphytic, elongate, sparsely branched, dorsiventrally compressed, 5 - 8mm broad, 3 - 4mm thick, green nearly glabrous except near growing apices, dictyostelic and having slender, dark sclerenchyma strands profusely scattered in the ground tissue. Paleae small, peltate, clathrate, gland-tipped and bearing a pair of prominent glandular hairs at base. Fronds borne in four irregular rows on the dorsal surface of the rhizome, articulate to small phyllopodia, dimorphic and simple. Each frond of the two lateral rows is associated with a basal branch as well as a pair of roots, but the other fronds are not. Sterile fronds spreading (perpendicular to the rhizome), stipitate (stipe 1.5 - 12.0cm long, 1.5 - 2.0cm thick, devoid of dorsal groove), with a thin, herbaceous, narrowly lanceolate lamina (30 - 50cm long and (1.5 -) 2.5 - 4.0cm broad) gradually tapered to a short acuminate apex and forming narrow tapered wings on the anterior region of the stipe; margin entire. Venation reticulate, having indistinct zigzag main veins and areoles possessing simple or forked included veinlets ending in hydathodes on the upper surface. Fertile fronds seasonal, erect (held parallel to the rhizome), clustered, filiform, devoid of lamina, 45 - 75cm long and 1.5mm broad. Sporangia aggregated in linear, exindusiate sori, one on either side of the naked midrib and extending all along it except for 5 - 12cm at the base and 1.0 - 1.5cm at the apex, mixed with filamentous paraphyses; annulus 15 cells long. Spores monolet, c. $35 \times 65 \mu\text{m}$, with spore coat not clearly differentiated into exine and perine, spinose.

The name is derived from Sanskrit: *Nistarika* meaning lamina-less (*ni* = devoid of; *starika* = lamina) and *bahupunctika* meaning several rows (*bahu* = many; *punctika* = having rows). The generic name refers to the lamina-less nature of the fertile fronds and the specific name to the many rowed arrangement of fronds on the rhizome.

MORPHOLOGY

Rhizome

N. bahupunctika grows in densely shaded forests among crowded undergrowth; it climbs up bases of woody shrubs and ultimately becomes semi-epiphytic as older parts of rhizome slough off. The rhizome is chlorophyllous, tenaciously attached by means of strong wiry roots borne in opposite pairs and horizontally encircling the support (Fig. 1a); the posterior roots extend to the ground. The paleae are dense in the younger regions but sparse elsewhere and are peltate, blackish, prominently clathrate, subtriangular in shape (Fig. 2b), c. $1-4 \times 0.5\text{mm}$, gland-tipped (Fig. 2c) and bearing a marginal uniseriate glandular hair (resembling the apex of the palea) on either side at the base. Ontogeny of the paleae is as in *Leptochilus axillaris* (Nayar 1963). The rhizome is hard and brittle, with parenchymatous ground tissue having faintly thickened silvery walls bearing prominent pits; slender sclerenchyma strands (1-7 cells thick, having occluded lumen and thick blackish walls bearing prominent pits) are scattered throughout. The vascular cylinder is a perforated dictyostele having slender cylindrical meristeles, and is eccentrically placed in the rhizome (cortex 5 or 6 cells thick on the ventral and 15-20 cells thick on the dorsal side). The endodermis is thin-walled but the inner walls of cells of ground tissue abutting on it are faintly thickened as in *Paraleptachilus decurrens* (not conspicuously thickened or dark brown as in *L. axillaris*). The dorsal half of the stelar cylinder is dissected by 4 or 5 irregular longitudinal rows of overlapping frond gaps (Fig. 3a). The vascular connection to the frond is shallowly channel-shaped and dissected by three irregular longitudinal rows of lacunae. Each frond of the two lateral rows is associated with two roots but the median fronds do not have any root association.

Study of apical organisation and morphogenesis in a large number of plants reveals that the patterns of growth and organogenesis in *N. bahupunctika* differ from

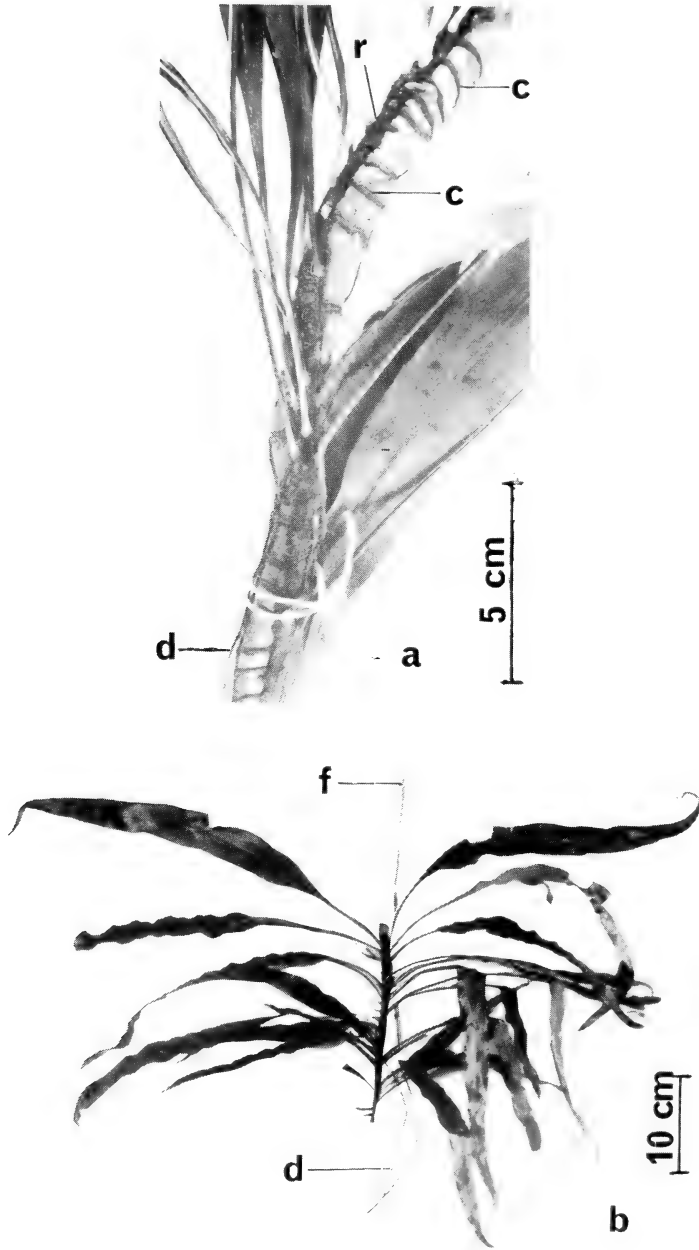


FIGURE 1. *Nistarika bahupunctika*: a, a portion of the rhizome clinging to the substratum and showing the clinging roots encircling the support; b, plant bearing a cluster of erect fertile fronds; (r, rhizome; c, clinging roots; f, fertile frond; d, posterior roots).

those found in several related genera such as *Drynaria*, *Microsorium*, *Paraleptochilus* and *Pyrrosia* (Nayar and Molly unpublished). In these genera the rhizome apex forks into two after producing each frond, and a frond primordium is soon differentiated on each of the daughter apices on the side facing the sister apex. The daughter apex nearest the older frond becomes dominant and continues growth of the rhizome while the other one away from the frond (along with the frond primordium on it) becomes sluggish and ultimately dormant. The frond primordium on the dominant daughter apex grows out as a frond, pushing away to one side the dormant daughter apex which then appears as a dormant branch of the rhizome associated with the developed frond. Thus fronds are alternate and in two opposite rows on the rhizome and each is associated with an abaxial branch. In *N. bahupunctika* also the rhizome apex forks equally into two after producing a frond, and each daughter apex differentiates a frond primordium next to the apical meristem (Fig. 6a). However, in contrast to the taxa mentioned above, both frond primordia grow out so that a pair of closely placed fronds result (Fig. 6b). One of the daughter apices then becomes sluggish and ultimately dormant but a second frond primordium (opposite the first one) is established on it and this primordium remains dormant. The other daughter apex of the rhizome becomes dominant and soon forks into two, each of the resultant daughter apices bearing a frond primordium (Fig. 6c). Frond primordia on both daughter apices grow out as developed fronds so that a second set of two fronds is formed (Fig. 6d) one beside the other. The daughter apex away from the dormant apex of the earlier forking becomes sluggish and ultimately dormant while its sister apex (which is now medianly placed) becomes dominant, continuing growth of rhizome (Fig. 6e). It forks again and the process is repeated (Figs. 6f,g,h). The dormant apex of each forking gets pushed away to one side as the dominant sister apices continue to grow. This pattern of growth results in four (in some cases appearing as three to five) irregular longitudinal rows of fronds on the dorsal side of rhizome. Of these the two lateral rows are developed fronds borne on the dormant daughter apices of successive forking of the rhizome apex and only these fronds have a branch associated with each (the branch being the dormant daughter apex of each forking) at its abaxial base. The median rows of fronds are borne on the dominant daughter apices which have continued growth and thus do not have any branch associated with them.

Fronds

The fronds are glabrous and glossy when mature; a few reduced paleae occur scattered on the stipe and main veins when young and a few minute (2-3 cells long) uniseriate non-glandular hairs on the lower surface of the lamina. Stomata are restricted to the lower epidermis and are copolomesoperigenous with the inner subsidiary cell narrow, having a smooth contour and nearly encircling the guard cells. The midrib is prominent and raised on both surfaces, but lateral veins are feeble and hidden in fresh material; the primary veins become somewhat evident in dried specimens. Primary lateral veins are 8-12mm apart and fork into divergent, strongly zigzag branches at the extreme base; the acroscopic branch is strongly oblique to the midrib and unites with the basiscopic basal branch of the next anterior vein to form a large costal areole, while the basiscopic branch is spreading, forking into equal divergent branches nearly $\frac{2}{3}$ rds to margin. Basiscopic branches of successive main veins are interconnected by zigzag secondary veins to form two or three rows of primary areoles which are further subdivided into two or three secondary areoles, each of which has a divided included veinlet. There is a nearly regular row of small marginal areoles and beyond them an occasional free-ending veinlet pointing to the margin. The large costal areoles possess a solitary included veinlet pointing to the midrib and commonly forked with the branches strongly divergent. All vein endings are

clavate and end in hydathodes in the upper epidermis. Fertile fronds are produced only during the dry season; they are usually 2-4 (up to 8) per apex of rhizome, held nearly parallel to the rhizome and extend a long way anterior to the rhizome apex. A lamina is totally absent and sporangia are borne directly on the midrib, with the sorus forming a continuous line on either side at the position where a lamina should have been. At the region of the sorus the midrib is grooved, with the soral placentum occupying the base of the groove (Fig. 4c,d).

Sporangia, spores and prothalli

The sporangia are mixed with slender, uniseriate, multicellular (5-6 cells), elongated, filamentous, gland-tipped paraphyses (Fig. 4d). The sporangial stalk is slender and elongated (5 cells long); annulus is 15 (14-16) cells long and prominently indurated. The spores (Fig. 2a) are bilateral, concavo-convex in lateral view, elliptic-oblong in polar view and $35 \times 65 \mu\text{m}$ in size but swelling to $40 \times 75 \mu\text{m}$ when acetolysed. The spore coat is golden-brown, less than $1.5 \mu\text{m}$ thick and densely spinose; spines irregularly aggregated in groups, $5-7 \mu\text{m}$ long, less than $1 \mu\text{m}$ thick, sometimes more or less curved, blunt and somewhat deciduous (mostly shed on acetolysis). The adult prothallus is of the ribbon-like branched type (Nayar and Kaur 1970) as in *Leptochilus*, forming small clustered patches. It is naked and one cell thick except for small cushions 2-4 cells thick borne in an irregular row medianly on the ribbon-like branches. Sex organs are borne on the lower surface of these cushions and are of the common type in Polypodiaceae.

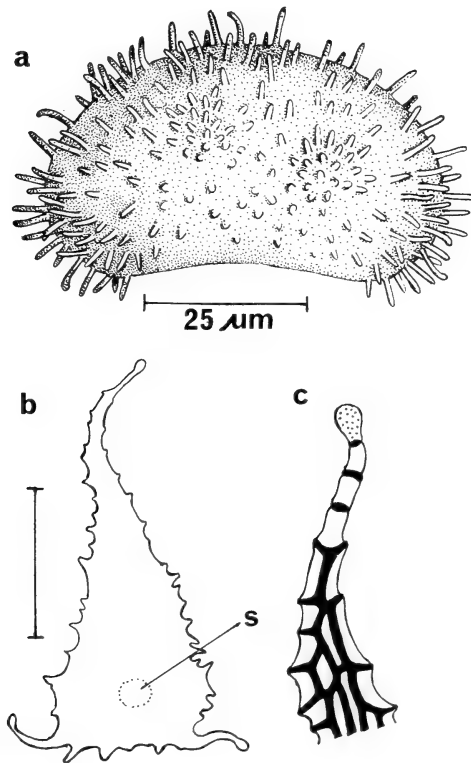


FIGURE 2. *Nistarika bahupunctika*: a, lateral view of spore; b, mature palea; c, apex of mature palea; (s, stalk of palea).

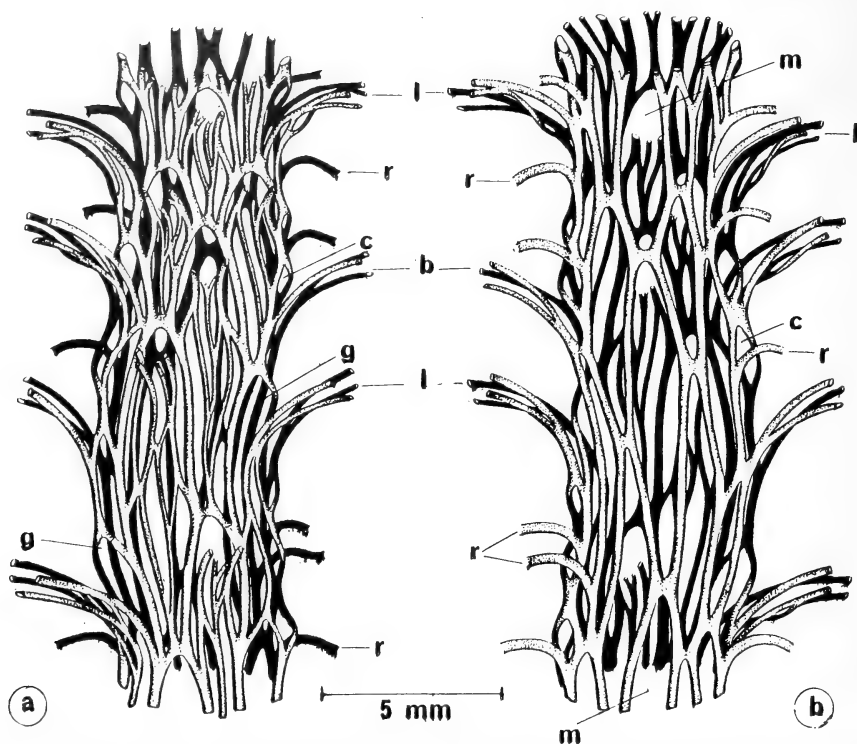


FIGURE 3. a, Dorsal view of vascular cylinder of a portion of rhizome; b, ventral view of vascular cylinder of the same portion of rhizome (b, branch trace; c, branch gap; g, frond gap; l, frond trace; m, medium ventral row of lacunae; r, root trace).

DISCUSSION

In general, Polypodiaceae *sensu stricto* are characterised by having a creeping dorsiventral rhizome bearing two dorsal rows of fronds (in some species, e.g. *Microsorium linguaeforme* and *Pseudodrynaria coronans*, the rows are so close as to appear as one), each articulated to a phyllopodium and associated with an abaxially lateral branch bud. *Oleandropsis* Copel. is exceptional in having an erect-growing slender radially symmetrical rhizome bearing several rows of fronds all around it. *Nistarika* differs from all other Polypodiaceous genera in having four rows of fronds restricted to the dorsal surface of a dorsiventral rhizome, and having branch buds associated with only the two lateral rows of fronds, the other fronds having no branch association. The growth habit of the plant which results in this characteristic arrangement of fronds and branches is unique, but only a variation from the common pattern found in the family (apical forking followed by one of the resultant branches becoming dormant). Sporangia are borne on the lamina of fertile fronds in all known Polypodiaceae; the lamina is highly reduced in some, but sporangia are restricted to the lamina region only and the midrib does not bear any sporangia. In contrast there is no trace of lamina in the fertile fronds of *Nistarika*; sporangia are borne directly on the midrib, and the fertile region forms a groove on either side, with the soral placentum seated at the base of the groove. However, the vascular supply to the sorus resembles the main lateral veins of the sterile lamina in its origin from the vascular bundles of the midrib, but remains well within the cortex of the midrib. Though a lamina is absent, the linear sori occupy the position that would be expected, were a lamina present. The combination of these unique characters excludes *Nistarika* from any known genus of ferns, justifying its separation as a new genus.

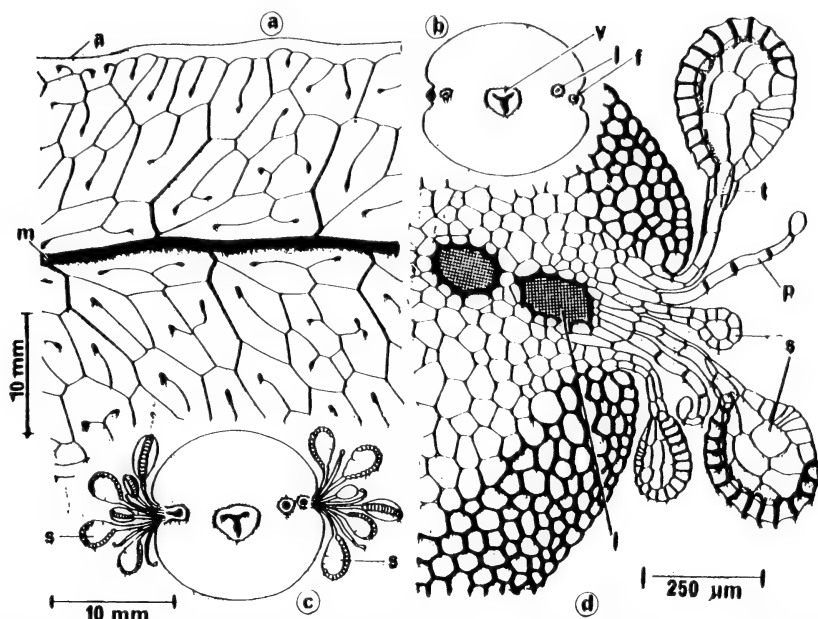


FIGURE 4. *Nistarika bahupunctika*: a, venation pattern, b, transection of a very young fertile frond showing initiation of sori; c, transection of a mature fertile frond; d, transection of sorus. (a, margin of frond; f, soral vascular supply; l, lateral vein subtending sorus; m, midrib; p, paraphysis; s, sporangium; t, third row of stalk cells; v, vascular bundle of midrib).

Nistarika resembles *Leptochilus* Kaulf. and *Paraleptochilus* Copel. except for the characteristic peculiarities of fertile frond, multi-rowed arrangement of fronds and eccentrically placed vascular bundle of rhizome. Though dried herbarium material of *N. bahupunctika* is confusingly similar in appearance to dried material of *L. axillaris* and *P. decurrens* forma *decurrens* and forma *lanceolata*, the resemblance is not so close with fresh material in the field. The habit of the four genera is characteristically different (Table 1) and *N. bahupunctika* differs from the others in its fertile fronds being clustered in groups and held vertically (parallel to the vertical substratum on which the plant grows, in contrast to being at c. 90° with the substratum in others); their laminaless nature renders them markedly more slender than the fertile fronds of other taxa. A comparison between *N. bahupunctika* and *L. axillaris*, *P. decurrens* forma *decurrens* and forma *lanceolata* is given in Table 1; Figure 5 gives a comparison of the venation pattern of the sterile frond. The venation of *P. decurrens* forma *lanceolata* is quite similar to *N. bahupunctika*, but that of *P. decurrens* forma *decurrens* is clearly different, particularly the very prominent nature of the primary lateral veins in the latter, and in the possession of a sheath of cells with coloured (dark-brown to blackish) deposits, making them more prominent. In possessing prominent sclerenchyma strands in the rhizome, and slender meristeles devoid of a prominent thick walled sheath, *N. bahupunctika* resembles *P. decurrens*; venation of sterile fronds and possession of filamentous paraphyses are additional similarities with *P. decurrens* forma *lanceolata*, but the semi-epiphytic habit, lack of sclerenchyma strands in the ground tissue of the stipe, possession of a thick-walled sheath around the vascular bundles of the stipe, the peltate nature of paleae, and spores bearing bacula-like large spines distinguish *N. bahupunctika* from *P. decurrens*. Though *N. bahupunctika* resembles *L. axillaris* in possessing similar paleae, absence of sclerenchyma strands in the stipe, possession of a thick walled sheath around the vascular bundles of the stipe, the venation pattern of the sterile leaf and possession of filamentous

paraphyses, it differs in possessing profuse sclerenchyma strands in the rhizome, lacking a thick walled sheath around meristeles, and having a stout and comparatively short rhizome which is tenaciously attached to the substratum. In the ribbon-like nature of its prothallus *N. bahupunctika* resembles both *Leptochilus* and *Paraleptochilus*, but it differs from both these genera in the pattern of its growth, lamina-less fertile fronds and bacula-like large spines on the spore wall.

TABLE 1. Comparative morphology of *Nistarika*, *Leptochilus* and *Paraleptochilus*

Characters	<i>Nistarika bahupunctika</i>	<i>Leptochilus axillaris</i>	<i>Paraleptochilus decurrens</i>	<i>P. decurrens</i> forma <i>lanceolata</i>
Habit	Restricted to densely shaded forest beds; initially terrestrial (creeping on soil) but later climbing up bases of supports and ultimately semi-epiphytic with rhizome not in contact with soil but bearing many roots extending to soil below.	Epiphytic in partially shaded areas, attached to tree trunks, growing throughout life with no connection to soil and wide creeping.	Terrestrial in densely shaded forest beds near streams and waterways; short creeping on rocky substrata.	Terrestrial in partially shaded forest beds; wide creeping on rocky or gravally soil but with a tendency to climb up supports.
Rhizome	Creeping vertically up, tenaciously attached to substratum ca. 8 mm thick, moderately elongated, hard, brittle, sparsely branched and having profuse sclerenchyma strands in ground tissue.	Creeping horizontally, loosely attached to substratum, ca. 5 mm thick, extensively elongated, soft, profusely branched, devoid of sclerenchyma.	Creeping horizontally, tenaciously attached to substratum, ca. 8 mm thick more or less short, sparsely branched, brittle, hard, having profuse sclerenchyma strands in ground tissue.	Creeping horizontally, loosely attached to substratum ca. 6 mm thick, much elongated, hard brittle, profusely branched and having profuse sclerenchyma strands in ground tissue.
Paleae	Peltate deciduous (absent in older regions).	Peltate, deciduous (absent in older regions).	Basally attached, dense all over, non-deciduous.	Basally attached, non-deciduous, but not dense in older regions.
Stele	Dictyostelic with many broad rather short perforations; meristeles slender, devoid of conspicuous sheath. Stelar cylinder eccentrically placed in the rhizome.	Dictyostelic with very narrow, much elongated perforations; meristeles thick, having a prominently conspicuous dark sheath of thick walled cells. Stelar cylinder not eccentrically placed in rhizome.	Dictyostelic with many broad, rather short perforations; meristeles slender, devoid of conspicuous sheath. Stele not eccentrically placed in rhizome.	Dictyostelic with many broad, rather short perforations; meristeles slender devoid of conspicuous sheath. Stele not eccentrically placed in rhizome.
Leaves	In 4 dorsal rows and only lateral ones associated with a branch each; stipe devoid of sclerenchyma strands but vascular bundles possessing a thick walled sheath. Fertile leaves clustered, devoid of lamina and bearing sporangia directly on midrib.	In 2 dorsal rows and each associated with a branch; stipe devoid of sclerenchyma strands but vascular bundles possessing thick-walled sheath. Fertile leaves not clustered, having very narrow lamina bearing sporangia; midrib devoid of sporangia.	In 2 dorsal rows and each associated with a branch; stipe having slender sclerenchyma strands in the ground tissue but vascular bundles devoid of thick-walled sheath. Fertile leaves not clustered, having very narrow lamina bearing sporangia; midrib devoid of sporangia.	In 2 dorsal rows and each associated with a branch; stipe having slender sclerenchyma strands in ground tissue but vascular bundles devoid of thick walled sheath. Fertile leaves not clustered having very narrow lamina bearing sporangia; midrib devoid of sporangia.
Spores	Bilateral, 35 x 65 μ , swelling to 40 x 70 μ on acetolysis; wall spinose with spines 7 μ long, blunt and uniformly thick throughout.	Bilateral, 30 x 54 μ , not swelling on acetolysis; wall spinulose with spinules 3 μ long, tapered to sharp apex.	Bilateral, 37 x 55 μ , not swelling on acetolysis; wall spinulose with spinules 3 μ long, slender, tapered to a sharp apex, deciduous, irregularly clustered.	Bilateral, 35 x 57 μ , not swelling on acetolysis; wall spinulose with spinules 5 μ long, slender, tapered to a sharp apex, aggregated in irregular groups.
Paraphyses	Filamentous, elongated, many cells long.	Filamentous, elongated, many cells long.	Absent.	Filamentous, elongated, many cells long.

N. bahupunctika resembles some species of *Bolbitis* Schott in its characteristic frond arrangement and association of branch buds with frond bases (Nayar and Kaur 1965). In addition several species of *Bolbitis* possess a highly reticulate venation similar to *N. bahupunctika* and a highly reduced fertile frond; also, at least some species of *Bolbitis* possess simple fronds. A tendency for the rhizome to climb vertically up bases of woody shrubs and for the plant to become semi-epiphytic like *N. bahupunctika* is seen in *B. appendiculata* (several such plants were noted, growing side by side with *N. bahupunctika* in Silent Valley), and a similar habit is reported for *B. sinensis* in Thailand (Hennipman 1977). In this context it is interesting to note that Hennipman (1977) in his monographic study of *Bolbitis* reported that *Leptochilus trifidus* v. A. v. R. of Sumatra is a *Bolbitis* and possibly a hybrid with *Leptochilus*, thereby suggesting some degree of relationship between the two genera. However, *Bolbitis* differs from *N. bahupunctika* as well as *Leptochilus* in its non-peltate paleae, non-articulated fronds, the stelar cylinder of the rhizome having an intact broad basal half, possession of foliar bulbils and chromosome number ($n = 41$, in contrast to $n = 36, 37$ in Polypodiaceae). Even the suspected hybrid, *L. trifidus*, possesses basally attached

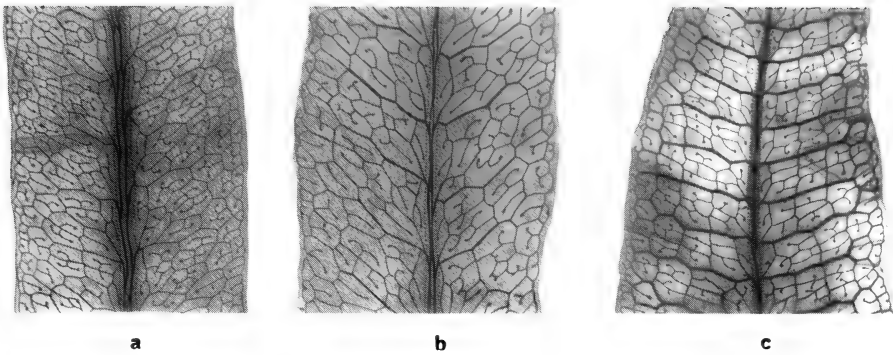


FIGURE 5. Venation of sterile frond of a, *Nistarika bahupunctika*, b, *Paraleptochilus decurrens* forma *lanceolata* and c, *P. decurrens* var. *decurrens*.

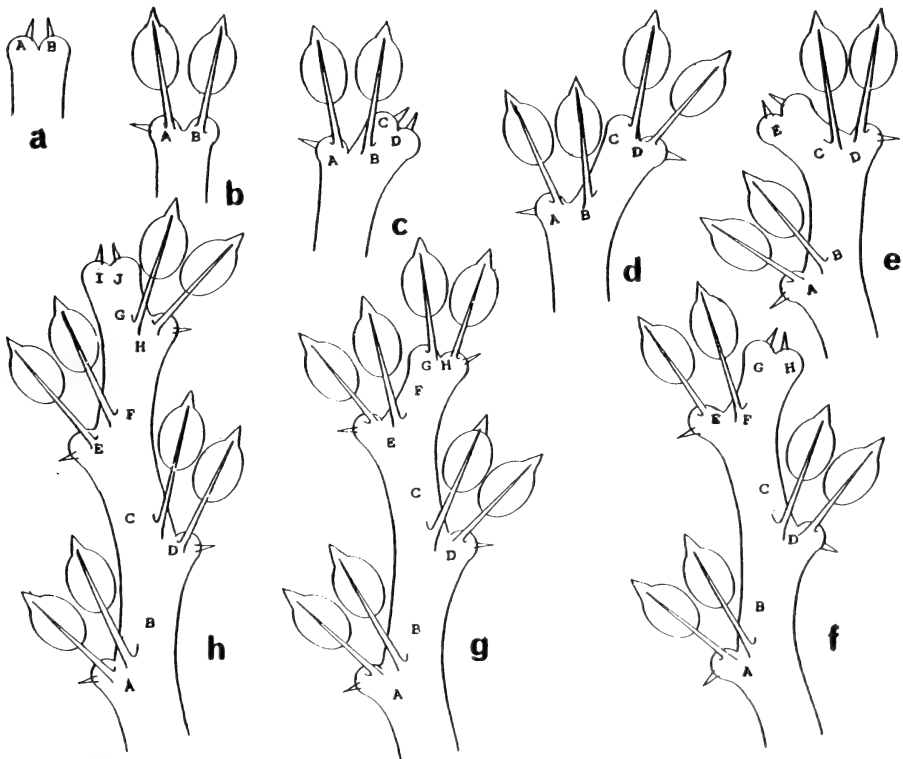


FIGURE 6. Diagrammatic representation of pattern of growth in *Nistarika bahupunctika* (for details see p. 36).

pseudo-peltate paleae bearing stout glandular marginal hairs, non-articulated leaves, foliar bulbils and a vascular cylinder having a prominent ventral meristele and prominently perinate spores, all characteristic of *Bolbitis*.

Nistarika is evidently related to *Leptochilus* and like it derived from *Microsorium*. Its epiphytic habit, elongated dorsiventral rhizome climbing vertically up supports and bearing stout long roots reaching down to the soil, simple lanceolate horizontally spreading leaves, reticulate venation with zigzag inconspicuous main veins which extend only part way up to the margin, filamentous paraphyses, 14-16 celled annulus and the large bilateral spores suggest *M. superficiale* (Bl.) Ching, but in the extreme reduction of the fertile lamina it is more advanced than *Microsorium* and even *Leptochilus*.

ACKNOWLEDGEMENTS

We should like to thank K. Kavanagh for correcting the Latin description.

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SHORT NOTE

CYRTOMIUM FALCATUM IN IRELAND

A single plant, identified as *Cyrtomium falcatum* (L.) Presl was located in west Cork, on the south coast of Ireland in December 1983. This is the first record of this species naturalized in Ireland. The plant grew in the seaspray zone of a 3m high cliff face with a public pathway just overhead, and had fourteen mature fronds, five young fronds and six dead ones. One dead frond measured 82cm. Young fronds were light green in colour and soft whereas the older ones were darker green and more cartilaginous. The brown scales were up to 1.3cm long and the pinnae up to 8cm long. The fronds tapered towards the top and less abruptly towards the bottom and were devoid of pinnae on the lower half. The pinnae had very distinct main veins with the numerous small orbicular sori scattered in between the secondary veins. Sori nearer the margins were closer together and smaller than those nearer the main vein. The indusium was circular and visible even in December. Of the five young circinate coiled fronds observed in December three were fully expanded four weeks later and the rudimentary sori were even faintly visible at that stage. Some pinnae while otherwise very healthy looking appeared to have been grazed (cf. specimen lodged in *DBN*), while on other fronds the pinnae were distorted and convoluted possibly as the result of seaspray or a virus or fungal infection.

It appears to be naturalized in this seaside location in west Cork. Likewise the species has been found in Australia colonising coastal cliffs and old cuttings near the sea and under boulders on the shore in the Isles of Scilly. The origin of this Irish specimen is unknown. The nearest likely source is a house a half mile away.

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THE GENERIC IDENTITY OF *POLYPODIUM BANAENSE*

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ABSTRACT

The species *Polypodium banaense* C.Chr. is transferred to *Crypsinus*. The recognition of a genus *Phymatopteris* Pic. Ser. (= *Phymatopsis* J. Sm.) separate from *Crypsinus* is discussed.

INTRODUCTION

In the course of my studies on the venation of Polypodiaceae, I visited the Paris herbarium and came across a few sheets of the indochinese fern originally published by Christensen (1934a) as *Polypodium banaense*. Subsequent character analysis of the venation, frond shape, rhizome scales and spores supports the view that the species belongs to *Crypsinus* (Polypodiaceae s.str.) as interpreted by Copeland (1947), and is therefore referred to that genus.

***Crypsinus banaensis* (C.Chr.) Hetterscheid comb. nov.**

Polypodium banaense C.Chr., Bull. Mus. (Hist. Nat., Paris), 2e sér, 1934: 105. *Phymatodes banaense* (C.Chr.) C.Chr. et Tard., Not. Syst., 8(4), 1939: 190. Tard. & C.Chr. in Lecomte; Fl. gén. Indoch., 7(2) fasc. 9, 1941: 468. *Paragramma banaensis* (C.Chr.) Ching, Sunyatsenia 5(4), 1940: 258. Type: Sallet (Herb. École sup. d'Agric. Hanoi, n. 3534), (BM, non vidi).

TAXONOMIC HISTORY

In the same year of its publication, Christensen listed *Polypodium banaense* in his Index Filicum (1934b, suppl. tert.) as belonging to *Polypodium* subg. *Microsorium*. Christensen & Tardieu-Blot (1939) transferred the species to *Phymatodes* Presl (= *Phymatosorus* Pic. Ser.) sect. *Paragramma*, on account of its indistinct venation, as opposed to sect. *Euphymatodes*. Ching (1940) accepted *Paragramma* Moore as a valid genus and proposed *Paragramma banaensis* (C.Chr.) Ching, which was not followed by Tardieu-Blot & Christensen (1941), who retained the species in *Phymatodes*, still regarding sect. *Paragramma* as part of it.

OBSERVATIONS

In addition to the descriptions given by Christensen (1934a) and Tardieu-Blot & Christensen (1941) the following observations are considered to be relevant. Contrary to Christensen's (1934a) remarks, the species is not dimorphic. Gradual frond elongation in both sterile and fertile specimens exists. The margin of small fronds is regularly notched (Fig. 1a,b), whereas this feature becomes irregular in fronds of intermediate lengths (Fig. 1c), and is absent in the largest fronds (Fig. 1d,e).

The venation (Fig. 1) consists essentially of the following parts: a series of narrow elongated areoles on either side of the rachis, in small fronds empty (Fig. 1a,b), in larger fronds sometimes containing one free recurrent vein (Fig. 1d,e). Each of these rows is bordered by a row of large more isodiametrical areoles. The included venation of the latter in the smallest fronds consists of one or two, usually free, excurrent veins (Fig. 1a,b). In all larger fronds the included venation is branched and anastomosed, thus developing smaller types of areoles (Fig. 1c,d,e), which are usually empty. Outside these larger areoles excurrent veins exist, which sometimes anastomose to form small marginal areoles.

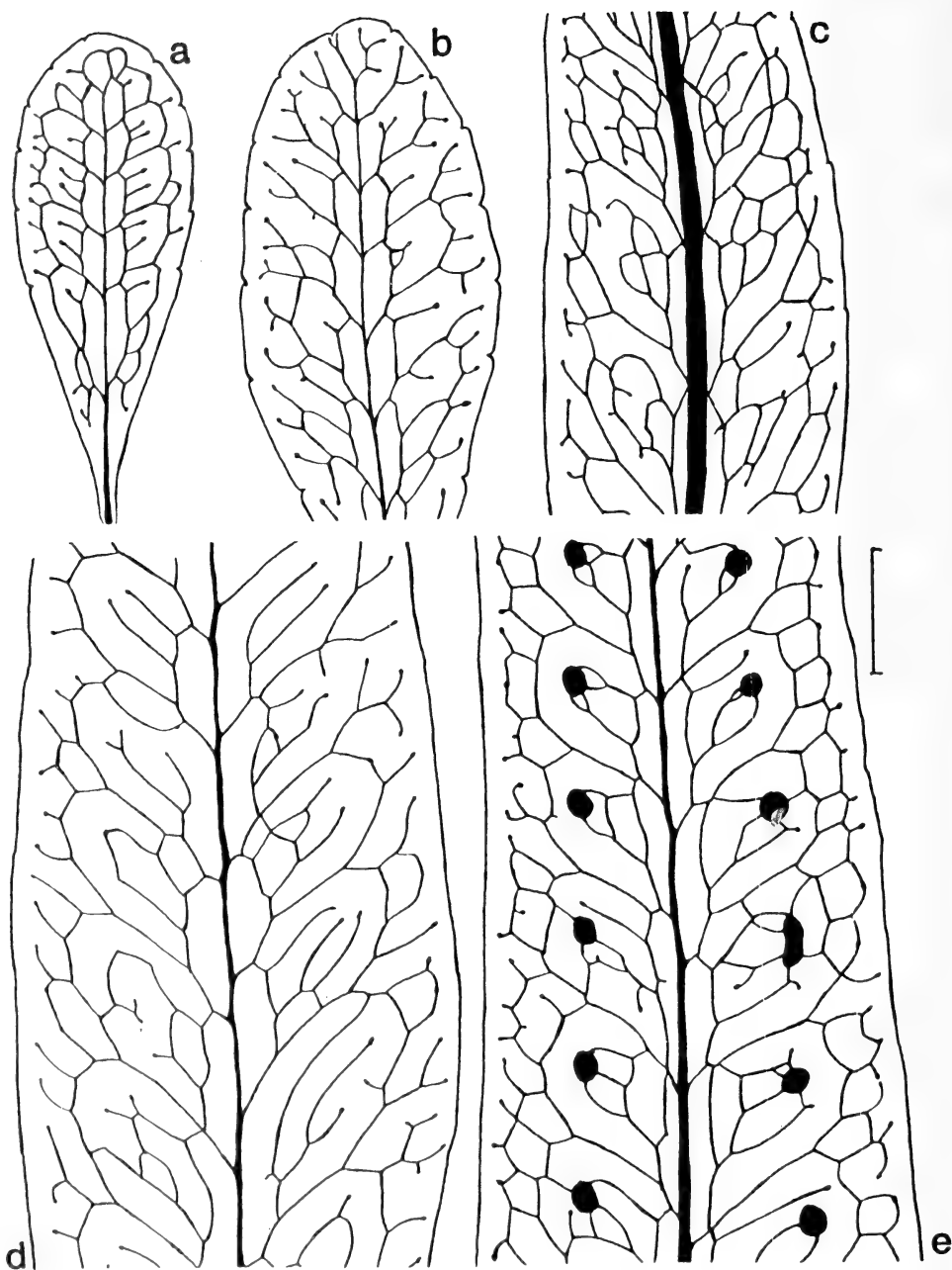


FIGURE 1. Venation patterns in *Crypsinus banaensis* (C.Ch.) Hetterscheid. a,b, small sterile fronds; c, intermediate sterile frond; d, large sterile frond; e, large fertile frond. (a,b, Sallet s.n. (P); c, Poilane 3524 (P); d,e, Poilane 5111 (P).). Scale bar: 5 mm.

The sori are situated in the larger areoles on fusion points in the included venation, one in each of them (Fig. 1e).

The spores are of the *Microsorium*-type (Hennipman & Roos 1983) and have a thick perispore as found in all species of *Crypsinus* and in some of the drynarioid ferns (pers. comm. E. Hennipman).

Contrary to Christensen (1934a) and Tardieu-Blot & Christensen (1941), I was unable to find receptacular paraphyses. The filiform paraphyses referred to are probably decapitated sporangial stalks which may be abundant in the sori.

DISCUSSION

A number of arguments indicate that inclusion of *Polypodium banaense* in either *Phymatosorus* or *Paragramma* is not justified. The venation is in essence different from that in both genera, the latter superficially resembling a goniophleboid pattern, but possessing a much more complicated included venation in the larger areoles, and developing from a very different series of blastogenetic stages (Mitsuta 1981, Hettterscheid & Hennipman 1984). The rhizome scales in both genera are clathrate, whereas those in *P. banaense* are opaque. The spores of *P. banaense* do not correspond to the type found in *Paragramma* or typical *Phymatosorus*, which possess the rather unique lepisorioid type (Hennipman & Roos 1983). Furthermore species of *Paragramma* possess peltate paraphyses of the type found in *Lepisorus*, which are absent in the present species.

The venation of the young fronds, the rhizome scales, the notching of the small fronds, and the spores all clearly correspond to features found in species of *Crypsinus*. Christensen (1934a) mentioned the strong similarity of *P. banaense* to *P. stenophyllum* Bl. (= *Crypsinus stenophyllus* (Bl.) Holtt.). He also compared the present species to *P. rhynchophyllum* Hook. (= *Phymatopteris* (*Crypsinus*) *rhynchophylla* (Hook.) Pic. Ser.).

The distinctions given by Ching (1964) to separate *Phymatopteris* from *Crypsinus* s.str., do not seem to be very conclusive. The species *Polypodium* (*Crypsinus*) *ensiforme* Thunb.* for instance, has a very striking goniophleboid venation (a character used by Ching to delineate *Crypsinus* s.str.), whereas the distinct lateral veins and large sori and pinnatifid frond point to an inclusion in *Phymatopteris*. Furthermore, in narrow frond parts of certain species of *Phymatopteris*, the venation reduces to a goniophleboid pattern (e.g. *P. albidosquamata* (Bl.) Pic. Ser.; Mitsuta 1984, Figs. 580-581). The "drynarioid" venation mentioned as a character of *Phymatopteris* is not useful, as a number of species of *Drynaria* have a goniophleboid venation (e.g. *D. parishii*, *D. sinica*; pers. comm. M.C. Roos). I therefore suggest that the genus *Crypsinus* be used in its broadest sense (Copeland 1947) until it is dealt with monographically.

The venation of *Crypsinus banaensis* shows an intriguing mixture of characters common to both *Crypsinus* and *Microgramma* Presl/ *Pleopeltis* Humb. et Bonpl. ex Willd. The small fronds contain a venation found in many young specimens of *Crypsinus* species or allies (e.g. *Pycnoloma* C.Chr.), the adult venation on the other hand shows a striking similarity to that found in species of *Microgramma* (compare Fig. 1e with de la Sota & Pérez-García 1982, Fig. 3a,b), or *Pleopeltis* (e.g. Mitsuta 1981, Fig. 6, 11, 17). In the light of morphogenesis of adult venations in blastogenetic frond series this is an interesting observation, showing that the *Microgramma* type of venation can develop via two different pathways, one, in most species of *Microgramma*, following the pattern found in *Polypodium* L. and *Goniophlebium* Presl, and another following part of the development in most *Crypsinus* species (Mitsuta 1984).

*The suggestion that *Phymatodes ensiformis* belongs to *Crypsinus* is debatable (it certainly is not a *Phymatodes*).

MATERIAL STUDIED

Poilane 3524 (P), 5111 (P), 6925 (P), 23913 (P); Sallet s.n. (P).

ACKNOWLEDGEMENTS

Thanks are due to Prof. Dr E. Hennipman for stimulating the preparation of the manuscript as well as its correction, and for providing information on the spores, and to Miss G.P. Verduyn and Mr M.C. Roos for additional information.

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REVIEW

ARKANSAS FERNS AND FERN ALLIES by W. Carl Taylor, illustrated by Paul W. Nelson. 262 pp. 240 x 207mm. Published by the Milwaukee Public Museum ISBN 0-89326-097-5 Arkansas. 1984. Price \$29.00.

This is a first-rate, beautifully produced book, the contents and presentation of which are an example to all local flora writers. I use the phrase 'local flora' with hesitation; Arkansas is larger than the whole of England by 3000 sq. miles! Introductory chapters, brief yet to the point, explain ferns and allied plants to the naturalist and layman; an illustrated glossary is a plus; pteridophyte distribution and ecology, discussed naturally in an Arkansas context, make interesting reading.

A well illustrated key is given to the 32 genera included. The bulk of the book is given to descriptions of these genera, keys to the 78 species found in Arkansas, and clear descriptions with a full page line-drawing of each species by one of the leading botanical artists of the present time. Not only is each page beautifully laid out but the close-up drawings are accurate and show what is required. As so many of the species are either grown in Britain or related to the European flora I expect the book to be as useful on this sides of the Atlantic as on the other.

A. C. JERMY

THE PTERIDOPHYTE HERBARIUM OF TRINITY COLLEGE DUBLIN

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ABSTRACT

The pteridophytes in the herbarium of Trinity College Dublin (**TCD**) are described. They comprise about 8000 specimens from 417 collectors and include previously unrecognised isotypes and holotypes. A list of major collectors is given with localities.

INTRODUCTION

The herbarium of Trinity College Dublin (**TCD**) was established around 1834, is the second largest herbarium in Ireland and contains at least 200,000 specimens (including lichens and bryophytes) with a notable collection of flowering plants and algae (see Holmgren, Keuken and Schofield, 1981). The only published list of collectors is that of Parnell (1982a) which relates solely to the rather small lichen collection. The pteridophyte collection is completely undocumented.

THE PTERIDOPHYTE COLLECTION AT **TCD**

Until recently the pteridophyte collection was ordered according to the scheme of Copeland (1947). Over the past two and a half years the collection has been re-ordered, to correspond with the scheme detailed by Crabbe, Jermy and Mickel (1975); at the same time nomenclature was revised to follow the most recent appropriate literature.

The collection totals approximately 8000 specimens, representing 228 genera collected largely during the 19th and early 20th centuries, with many specimens from remote and rarely visited localities, for example New Caledonia, St Helena and Oahu in the Hawaiian Islands. Perhaps the most interesting small collection is that made by W.J. Sollas on a famous Royal Society expedition in 1896, which made deep borings into the coral of Funafuti, a small island in the SW Pacific near the Ellice Islands, thereby confirming Darwin's theories on the origins of coral reefs.

Approximately one eighth of the specimens in **TCD** come from the British Isles and, of these, one sixth were collected by the previous curator Prof. D.A. Webb. The European collection (including the British Isles) totals some 1400 specimens and is the one most added to in the latter part of this century. The collection also has a large number of specimens from Australasia, India, Sri Lanka and tropical South America.

Revision has indicated that the collection contains a number of isotypes and some holotypes. The majority of the 417 collectors among the pteridophytes are also represented in the phanerogamic collection. The most prolific and important collectors are listed below; countries of origin are given after the collector. South Africa is taken to exclude South West Africa (Namibia) but to include Lesotho, Swaziland and all Bantustans.

Archer, W. (Tasmania); Babington, C.C. (China and Japan); Backhouse, J. (Mauritius); Ball, J. (Algeria, France, Germany, Italy, Morocco, Sicily, Switzerland, Spain); Ball, P.W. & Chater, A.O. (Spain, Yugoslavia); Barnard, J.C. (Trinidad); Barter, C. (Fernando Po, Sierra Leone); Beckett, T.W.N. (Sri Lanka); Brown, W. (China, west coast of Africa); Buckley, S.B. (U.S.A.); Claussen, P. (Brazil); Cooper, T. (South Africa); Coulter, T. (Britain, Ireland, Madeira, Mexico, Panama, U.S.A.); Cuming, H. (Chile, Galapagos Islands, Malacca, Panama, Philippines, Pitcairn Island, Society Islands, St Helena); Deplanche, ? (New Caledonia); Drège, C.F. (South Africa); Drummond, T. (Canada, U.S.A.); Eaton, D.C. (Filices Boreali-Americanae); Edwards, Rev. ? (Jamaica); Fendler, A. (New Mexico, Panama, Venezuela); Gardner, G. (Brazil, India, Sri Lanka); Gerrard, W.T. (South Africa); Gerrard, W.T. & McKen, M.J. (South Africa); Griffith, W. (China, India, Malaysia, Malasia,

Philippines, Sri Lanka); Gunn, R.G. (Tasmania); Halliday, G. (Britain, Ireland); Harvey, W.H. (Australia, Chile, Fiji, Friendly Islands, Great Britain, Ireland, Madeira, New Zealand, Sri Lanka, South Africa, Switzerland, Tasmania, U.S.A.); Haughton, ? (St Helena); Hind, W.M. (Britain, Ireland); Hooker, J.D. (Argentina, Australia, Brazil, Guyana, Canada, Columbia, Falkland Islands, Guatemala, Hawaii, Hermite Island, India, Jamaica, Java, Kerguelen Island, Madeira, Mauritius, Norfolk Island, Oahu, Peru, St Helena, Sandwich Islands, Sierra Leone, South Africa, Sri Lanka, Switzerland, Tasmania, Trinidad); Hooker, J.D. & Thomson, T. (Bangladesh, India); Hooker, W.J. (*ex. herb.* Jamaica, Madagascar, Madeira, Mauritius, Sri Lanka); Hunt, T.C. (Azores); Hutton, H. (South Africa); Jameson, W. (Brazil, Ecuador, Mexico); Jenkins, F. (India); Johnson, E. (India); Kelly, D.L. (Jamaica, Ireland); Kerr, A.F.G. (Siam); Kirk, T. (*ex. herb.* Britain); Lechler, W. (Chile, Peru — a set issued by Hohenacker); Linden, J.J. (Nicaragua, Venezuela); Lobb, T. (Java, Malaya); Lyaill, D. (Australia, Greenland, New Zealand, South Sea Islands); Mackay, T.J. (Ireland); Mathews, A. (Peru, Society Islands); Miers, J. (Brazil); Oldham, T. (India); Oakes, W. (U.S.A.); Pearson, C. (Ireland); Poeppig, E.F. (Brazil, Chile, Cuba, Peru, U.S.A.); Pringle, A. (Ireland); Sartwell, H.P. (U.S.A.); Schomburgk, R.H. (Guyana); Schultz, N. (Norfolk Island); Simons, ? (India); Sinclair, A. (some labelled *ex. herb.* W. Gourlie, New Zealand, Mexico, Panama); Spruce, R. (Brazil, Ecuador, Peru); Strange, F. (Australia); Thomson, T. (India); Thwaites, G.H.K. (Sri Lanka); Vieillard, E. (New Caledonia); Wallich, N. (India, Malaysia and some enigmatically labelled East Indies (see Van Steenis [1950-]); Webb, D.A. (Australia, Austria, Britain, Bulgaria, France, Ireland, Italy, Yugoslavia, Madeira, Portugal, Spain, Sweden, Switzerland, Turkey); Wright, ? Miss (the daughter of C.H. Wright) (Britain); Wright, C. (Cuba, New Mexico, South Africa); Wright, E.P. (Ireland).

The pteridophyte collection is now in the process of computerisation (Parnell 1982b), a process which it is hoped will eventually be extended to the whole herbarium. Further details of the collection, its contents and additional information on collectors are available on request

ACKNOWLEDGEMENTS

I would like to thank Miss E. Lowe for extracting some of the data relating to collectors from the herbarium, Dr D.L. Kelly and Professor D.H.S. Richardson for helpful comments on an early draft of this manuscript.

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'SPOROPHYLL-PTERYX' IN AFRICAN AND AMERICAN *SELAGINELLA*

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ABSTRACT

Vertical/oblique projections are reported as occurring on the adaxial surfaces of sporophylls of fourteen West African and twenty South American species of *Selaginella*. We propose that this projection be called 'sporophyll-pteryx'.

INTRODUCTION

The genus *Selaginella* P. Beauv. is made up of isophyllous and anisophyllous species. The strobili of both the isophyllous and anisophyllous species are terminal, on branches and/or branchlets. The anisophyllous species possess one of two basic types of strobili depending on whether the distinct anisophylly of the vegetative leaves is continued into the reproductive structures or not.

The tetragonous strobilus has distinct anisophylly of the vegetative leaves which is not continued into the reproductive structures; the sporophylls are all uniform or subuniform. In contrast, where the anisophylly of the vegetative leaves is continued into the reproductive structures, dimorphic sporophylls (Fig. 1b-e) result in a bilateral strobilus.

There are two forms of bilateral strobili — resupinate and non-resupinate strobili. In the resupinate strobili (Fig. 1a) the smaller sporophylls are in the same plane as the larger lateral vegetative leaves, while the larger sporophylls are in the same plane as the smaller median vegetative leaves. The non-resupinate strobili have the smaller sporophylls in the same plane as the smaller median vegetative leaves, while the larger sporophylls are in the same plane as the larger lateral vegetative leaves.

This paper reports on the presence of vertical/oblique projections on the adaxial surfaces of sporophylls in a number of West African and South American species of *Selaginella* which have been found to possess the bilateral resupinate form of strobilus.

OBSERVATIONS

During a re-investigation of the West African species of *Selaginella* it has been found that a substantial number of them possess the bilateral resupinate form of strobilus. Critical examination of the sporophylls of these species has revealed that the larger sporophylls are of an unusual form. They have a vertical/oblique projection on their adaxial surfaces.

Alston (1959), who gave the first comprehensive account of the genus *Selaginella* in West Africa, listed 20 species. All the 20 species have been examined for the presence of this vertical/oblique projection on the adaxial surface of the sporophyll. Six of these have tetragonous strobili while 14 have the bilateral resupinate form. The projection was found in all the 14 species (Table I) possessing the bilateral resupinate strobili.

One hundred and twenty-eight of the 133 species of *Selaginella* listed by Alston et al. (1981) in South America have also been examined for this projection. Twenty of these have bilateral resupinate form of strobili with the projection on the adaxial surface of their sporophylls (Table II).

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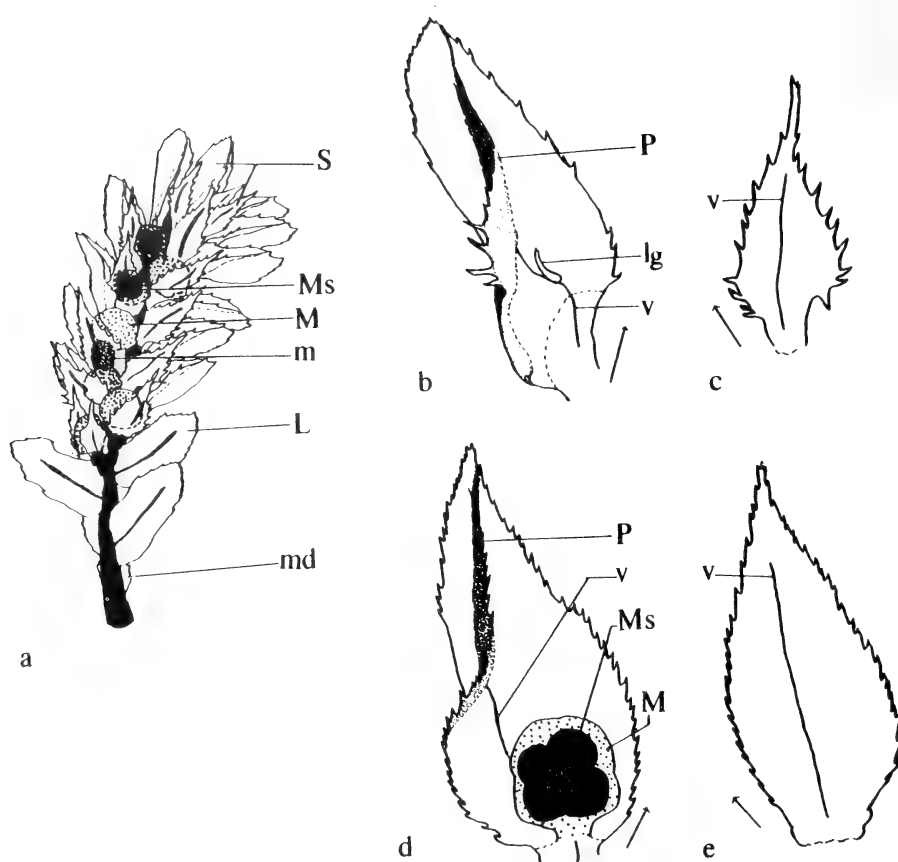


FIGURE 1.

a. A bilateral resupinate strobilus of *S. molliceps* Spring under-surface view (Exell, 500, BM); b-c. dimorphic sporophylls of *S. leoneensis* Hieron. (Harley, F161, BM); b, dorsal sporophyll showing complete sporophyll-ptyx and position of ligule in relation to sporophyll-ptyx; c, ventral sporophyll; d-e. dimorphic sporophylls of *S. hartwegiana* Spring (from Type specimen, Hartweg 1477, BM); d, dorsal sporophyll showing partial sporophyll-ptyx; e, ventral sporophyll. a, x12, b-e, x30 (L = lateral leaf, lg = ligule, M = megasporangia, Ms = megaspore, m = microsporangium, md = median leaf, P = sporophyll-ptyx, S = sporophylls, v = midvein). (Arrows indicate the relative positions of the sporophylls to the axis of the strobilus and point to the apex of the strobilus).

The presence of the projection on the adaxial surface of the larger sporophylls gives these sporophylls an unusual and asymmetrical shape. We suggest that the projection is the result of a fold of the outer half of the sporophyll onto the adaxial surface of itself. It appears that some fusion of the laminal tissue has occurred within the fold. About a quarter or so of the folded side of the sporophyll stands out and it is this portion that is seen as the vertical/oblique projection on the adaxial surface of the sporophyll. We propose that this projection be called 'sporophyll-ptyx'; 'ptyx', from the Greek, means flap or fold.

The extent to which the sporophyll appears to have been folded and the extent of fusion of its surfaces has resulted in two main forms of sporophyll-ptyx. These we are calling partial, and complete, sporophyll-ptyx (Figs. 1d and b). The partial sporophyll-ptyx occurs from the apex along about one third the length of the mid-

vein, then extends obliquely to the edge about midway along the length of the outer side of the sporophyll. The fusion of the laminal tissue of the surfaces is incomplete, thus the sporophyll-ptyx, in this case, can easily be lifted and moved back to reveal parts of the adaxial surfaces of the fold. The complete sporophyll-ptyx occurs from the apex along about two-thirds the length of the mid-vein, then extends obliquely to the edge of the outer side, as far as the base of the sporophyll. The fusion of the laminal tissue of the surfaces of the folded side is more or less complete except the portion forming the sporophyll-ptyx. Any attempt to lift and move the sporophyll-ptyx back to reveal parts of the adaxial surfaces of the fold results in damaging the sporophyll.

Thirteen out of the 14 West African species possess the complete sporophyll-ptyx, whilst the remaining one species has the partial sporophyll-ptyx (Table I). Seven of the 20 South American species have complete sporophyll-ptyx; the remaining 13 species have partial sporophyll-ptyx (Table II).

TABLE 1. Species of West African *Selaginella* with sporophyll-ptyx

<i>S. abyssinica</i> Spring	C	<i>S. protensa</i> Alston	C
<i>S. blepharophylla</i> Alston	C	<i>S. soyauxii</i> Hieron.	C
<i>S. buchholzii</i> Hieron.	C	<i>S. squarrosa</i> Bak.	C
<i>S. kalbreyeri</i> Bak.	P	<i>S. subcordata</i> A.Br. ex Kuhn.	C
<i>S. leoneensis</i> Hieron.	C	<i>S. tenerima</i> A.Br. ex Kuhn.	C
<i>S. mollerii</i> Hieron.	C	<i>S. thomensis</i> Alston	C
<i>S. molliceps</i> Spring	C	<i>S. zechii</i> Hieron.	C

TABLE II. Species of South American *Selaginella* with sporophyll-ptyx

<i>S. cavifolia</i> A.Br.	P	<i>S. moritziana</i> Spring ex Klotzsch	P
<i>S. cladorrhizans</i> A.Br.	P	<i>S. novae-hollandiae</i> (Sw.) Spring	P
<i>S. flacca</i> Alston	C	<i>S. pearcei</i> Bak.	P
<i>S. flagellata</i> Spring	C	<i>S. popayanensis</i> Hieron.	P
<i>S. glossophylla</i> Alston ex Crabbe & Jermy	P	<i>S. porelloides</i> (Lam.) Spring	C
<i>S. hartwegiana</i> Spring	P	<i>S. radiata</i> (Aubl.) Spring	P
<i>S. lychnuchus</i> Spring	C	<i>S. ramosissima</i> Bak.	C
<i>S. macilenta</i> Bak.	C	<i>S. seemannii</i> Bak.	P
<i>S. meridensis</i> Alston	P	<i>S. simplex</i> Bak.	C
<i>S. mollis</i> A.Br.	P	<i>S. substipitata</i> Spring	P

C = complete sporophyll-ptyx

P = partial sporophyll-ptyx

DISCUSSION

Mukhopadhyay and Sen (1981) have reported on the presence of a laminal flap in four species of *Selaginella* – *S. bisulcata* Spring, *S. reticulata* (Hook and Grev.) Spring, *S. tenera* (Hook and Grev.) Spring and *S. subdiaphana* (Wall.) Spring — in India. Reporting on the presence of the flap in the Indian species, they stated that "the flap is situated next to the ligule" and that "it is a continuation of the lamina and extends from the base towards the distal region of the bract or the sporophyll along the midrib". This flap is the same as the sporophyll-ptyx we are describing in the West African and South American species of *Selaginella*.

Our investigation, however, reveals that the sporophyll-ptyrux is not situated next to the ligule (Fig. 1b). Some of them, upon first glance, appear to be situated next to the ligule, for they appear to extend from the apex, along the whole length of the mid-vein, to the base of the sporophyll. However, critical examination has shown that they are not situated next to the ligule. They do not extend along the whole length of the mid-vein but are the same as we have described for the complete sporophyll-ptyrux above.

The possession of sporophyll-ptyrux in these species of *Selaginella* is seen as an additional character which can be used in the systematics of the genus *Selaginella*. The presence of the sporophyll-ptyrux in 14 West African and 20 South American species of *Selaginella*, in addition to the four species from India, makes it seem highly likely that species of *Selaginella* from other parts of the world will be found to possess the sporophyll-ptyrux.

ACKNOWLEDGEMENTS

The authors are grateful to Mr A.C. Jermy, Miss J.M. Camus and Miss A.M. Paul of the British Museum (Natural History) for the provision of herbarium material and for constant encouragement. We are also grateful to Dr D.S. Edwards of the Botany Department, University of Cape Coast, Ghana, for sending us collections from Ghana, West Africa.

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BRITISH PTERIDOPHYTE RECORDS

Compiled by A.J. Worland, BPS Recorder

The following records have been received and are additions to the *Atlas of Ferns* (1978); I am grateful to all concerned. As in previous years, the records are presented thus; 100km square/10km square followed by the recorder's name. WV27 refers to Guernsey and WV65 to Jersey (Channel Islands).

POST 1950

- 5.2 *Selaginella kraussiana* WV27 W. Bennert
- 7.4x3 *Equisetum* × *litorale* WV27 W. Bennert, 27/60 H. McHaffie & C.N. Page, 37/04 H. McHaffie
- 10.1 *Osmunda regalis* WV27 W. Bennert
- 13.1 *Adiantum-capillus-veneris* 13/64 J. Crighton
- 16.1 *Polypodium vulgare* WV65 A.J. Worland
- 16.2x1 *Polypodium* × *mantoniae* 42/57 R.P.H. Lamb
- 16.3 *Polypodium australe* WV65 A.J. Worland
- 17.1 *Pteridium aquilinum* WV27 W. Bennert, WV65 A.J. Worland
- 19.1 *Phegopteris connectilis* 38/44 D. Welch
- 20.1 *Oreopteris limbosperma* WV65 A.J. Worland
- 22.1 *Athyrium filix-femina* 48/02 A.O. Chater
- 26.2x3 *Polystichum* × *bicknellii* WV27 W. Bennert
- 26.2 *Polystichum aculeatum* WV27 W. Bennert
- 26.3 *Polystichum setiferum* WV27 W. Bennert, WV65 A.J. Worland
- 27.2 *Dryopteris filix-mas* WV27 W. Bennert, WV65 A.J. Worland
- 27.1x2 *Dryopteris* × *mantoniae* 23/60 P.M. Benoit
- 27.3 *Dryopteris affinis* WV65 A.J. Worland
- 27.9x8 *Dryopteris* × *daweveri* 63/42 A. Willmot
- 28.1 *Blechnum spicant* 43/33 A. Willmot

ASPLENIUM PUNJABENSE SP. NOV. AND ITS SIGNIFICANCE FOR THE STATUS OF CETERACH AND CETERACHOPSIS

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ABSTRACT

A new spleenwort, *Asplenium punjabense* Bir, Fras.-Jenk. & Lovis and a new hybrid, *Asplenium* × *geni-coalitum* Fras.-Jenk. (= *A. dalhousiae* × *A. punjabense*), are described. *A. punjabense* is a hexaploid sexual species presumed to be derived from *A. ceterach* subsp. *ceterach* and *A. dalhousiae*. *Ceterach* and *Ceterachopsis* are given subgeneric status and their species are enumerated under the two subgenera. Five new specific combinations are made and chromosome numbers are recorded for four species of *Ceterach* for which no previous cytological reports exist. The significance of the existence of an allopolyploid species combining members of the sub-genera *Ceterach* and *Ceterachopsis* is discussed.

INTRODUCTION

Ceterach Willd. in the family Aspleniaceae Mett. ex Frank is a small group previously treated by most authors as a genus and containing, when circumscribed in a wide sense, about twelve morphologically close species (see Copeland 1947 and below). From the Himalaya, in addition to *Ceterach officinarum* DC. (= *A. ceterach* L.), the two other species usually attributed to *Ceterach* are *C. dalhousiae* (Hook.) C.Ch. (= *A. dalhousiae* Hook.) and *C. paucivenosum* Ching (= *A. paucivenosum* (Ching) Bir). Of these species, the last two, *A. dalhousiae* and *A. paucivenosum*, have been further separated into another genus or group, *Ceterachopsis* J. Smith, whose main feature of distinction is the presence of an indusium and the absence of scales on the lamina unlike in the members of *Ceterach* sensu stricto. However all three species (as indeed can all the species contained within *Ceterach* and *Ceterachopsis*) can equally well fall within normal definitions of *Asplenium* and according to Copeland (1947: 169), "It is simply impossible to define *Asplenium* so as to exclude them, and difficult to define *Ceterach* so as to include them". He also stated, "While I entertain no doubt as to the propriety of leaving *A. dalhousiae* in *Asplenium* its affinity to *Ceterach* is obvious, and makes evident the place in *Asplenium* (*Ceterachopsis* J. Smith) from which *Ceterach* was evolved".

A good deal of discussion has taken place as to the desirability of separating *Ceterach* and other genera from *Asplenium*, especially in view of the existence of wild intergeneric hybrids of *Asplenium* with *Ceterach*, *Camptosorus* and *Phyllitis* (= *Scolopendrium*) (Lovis 1973, Bennert & Meyer 1974). Furthermore, a hybrid between *Asplenium* and *Pleurosorus*, and another which is in effect trigeneric, combining together genomes from *Asplenium*, *Camptosorus* and *Phyllitis*, have both been synthesised (Lovis 1973). As a result a number of authors have suggested the merging of these and other genera as subgenera within *Asplenium*; the most important discussions are those of Copeland (1947), for *Ceterachopsis*, *Phyllitis*, *Asplenidictyum*, *Neottopteris*, *Ceterach*, *Camptosorus* etc.; Bir (1962, 1963) and Bir in Mehra and Bir (1964) for *Ceterach* and *Ceterachopsis*; Vida (1963), for *Phyllitis* and *Ceterach*; and

Lovis & Vida (1969), for *Phyllitis*, *Ceterach*, *Camptosorus* and *Pleurosorus*. Lovis (1973), however, puts the case both for and against merging these genera within *Asplenium*, and more recently some important authors working on the Aspleniaceae have kept them separate (e.g. Lovis 1977, Pichi Sermolli 1977 and Reichstein 1981) and it may well be that the presence or absence of intergeneric hybrids in this particular family may not be a useful guide to generic limits bearing in mind the distinct morphology of these discrete groups. Clearly though the generic status of all the groups is at least open to doubt and they may either be maintained, or reduced to subgenera, as has been done for all of them at some stage; Bir (1963) and Bir in Mehra & Bir (1964: 158-159), for example, has treated *Neottopteris* and *Asplenidictyum* as subgenera of *Asplenium*, even in the absence of intergeneric hybrids, because they are considerably closer in morphology to *Asplenium* than to the other genera discussed here and have long been included in it by many authors (see Christensen 1905-6: 98, 432, Copeland 1947 etc.). More recently, the situation has been complicated by the description of *Sinephropteris* as distinct from *Schaffneria* (Mickel 1976) and by the finding by Kurita (1972) that *Boniniella* has $n = 76$ ($x = 38$), in contrast to all the rest of the Aspleniaceae which, with the exception of a small group of taxa in the *A. unilaterale* complex, uniformly have $x = 36$.

In this paper, mainly for the sake of convenience, *Ceterach* and *Ceterachopsis* are included within *Asplenium* as subgenera even though the present trend in European literature is to maintain *Ceterach* as a genus. Further discussion follows later in the paper as to the alternatives and the separation of the two subgenera from each other.

OBSERVATIONS AND NEW TAXA

Bir (1962, 1963: 42-43) and Bir in Mehra and Bir (1964: 158-159) has discussed why he followed Christensen (1905-1906) and Copeland (1947) with regard to sinking *Ceterachopsis* (but not *Ceterach*) within *Asplenium*. While outlining the evolution of various morphological groups within *Asplenium*, he reported (sub *A. ceterach*) the presence of some Himalayan specimens from Kulu in the Western Himalaya which had a morphology intermediate between *A. ceterach* on the one hand and *A. dalhousiae* on the other. The presence of plants with their morphology thus intermediate between *Ceterach* and *Ceterachopsis* had potential significance: this finding apparently supported Copeland's statements and indicated how *Ceterach* could possibly have evolved from *Asplenium* through *A. dalhousiae*. Therefore Bir recognised *Ceterachopsis* as a subgenus of *Asplenium*, *A. dalhousiae* Hook. being the type species and *A. paucivenosum* being its only other member then known. More recently, however, Löve et al. (1977) have followed Ching (1940) in recognising *Ceterachopsis* as a genus.

Subsequent to Bir's report of intermediates a new spleenwort was discovered by J.D. Lovis in a spore sowing made at Leeds from a sheet of *Asplenium trichomanes* subsp. *trichomanes* collected by Bir from Kulu in the late 1950's. The origin of this contaminant, which was clearly distinct from any other *Ceterach* in culture at Leeds at that time was at first mysterious, but investigation subsequently revealed an excellent match in a single specimen collected by Bir at the same time in the same locality and donated to the BM in the same batch. The source of the stray spores was then obvious. This new species showed some characteristics intermediate between *A. ceterach* and *A. dalhousiae* and it became clear that it was the origin of Bir's earlier observation (Bir 1963). Lovis studied its cytology and found the taxon to be hexaploid ($n = 108$). This finding, together with the intermediate morphology, made it probable that it had arisen by chromosome doubling in a triploid hybrid of *A. ceterach* subsp. *ceterach* (tetraploid, $n = 72$) and *Asplenium dalhousiae* (diploid, $n = 36$) both of which are sympatric with it in the area. The tetraploid ancestral species, *Asplenium ceterach* subsp. *ceterach*, is not

uncommon, being scattered throughout the slightly drier parts of the Western Himalaya, between 1300 and 2700m altitude, extending from Afghanistan to Tehri Garhwal, including the Kulu area (Hope 1901-1902). Bir (1959) has also published on its presence in the Kulu area. The diploid ancestral species, *A. dalhousiae*, is considerably commoner and is abundant around Kulu, but its distribution extends further eastwards into the wetter parts of the Himalaya, from Afghanistan to W & C Nepal between 1,000 and 2,500m altitude (see Hope 1901-1902 and also, more recently, Mehra & Bir 1957, Bir 1959, 1962, Bir & Shukla 1967 and others).

Since the new fern was first discovered in a spore culture made from specimens collected in the Kulu valley, which was part of the state of Punjab, India at the time of collection, it has been given the specific epithet, '*punjabense*', but the area now forms part of the state of Himachal Pradesh and is described as such in the citation of specimens. It is fortunate that one of us (Fraser-Jenkins) was able to find the species growing wild at the type locality as it had previously been known only from the spontaneous spore-culture material and single herbarium specimen. Without further study in the field, including the making of more wild collections and the discovery of other herbarium specimens by Fraser-Jenkins it was not possible to establish that the plant was firmly established, rather than of evanescent occurrence, in nature (cf. the status of *Asplenium eberlei*, Eberle 1967, Meyer 1967).

The diagnosis of the new fern is as follows:

Asplenium punjabense Bir, Fraser-Jenkins et Lovis, **spec. nov.** Filix sempervirens; morphologia inter *Asplenium dalhousiae* Hooker et *Asplenium ceterach* L. interjecta; differt a specie prima facie abaxiali laminae paleacea et anastomosibus nonnullis venarum propter marginem laminae: a specie altera indusio suppetente et paleis facia abaxiali laminae minus densis differt; ab utraque specie sporis majoribus atque numero chromosomico hexaploido, scilicet paribus chromosomatum meiosi regularibus 108 in reproductione sexuali differt.

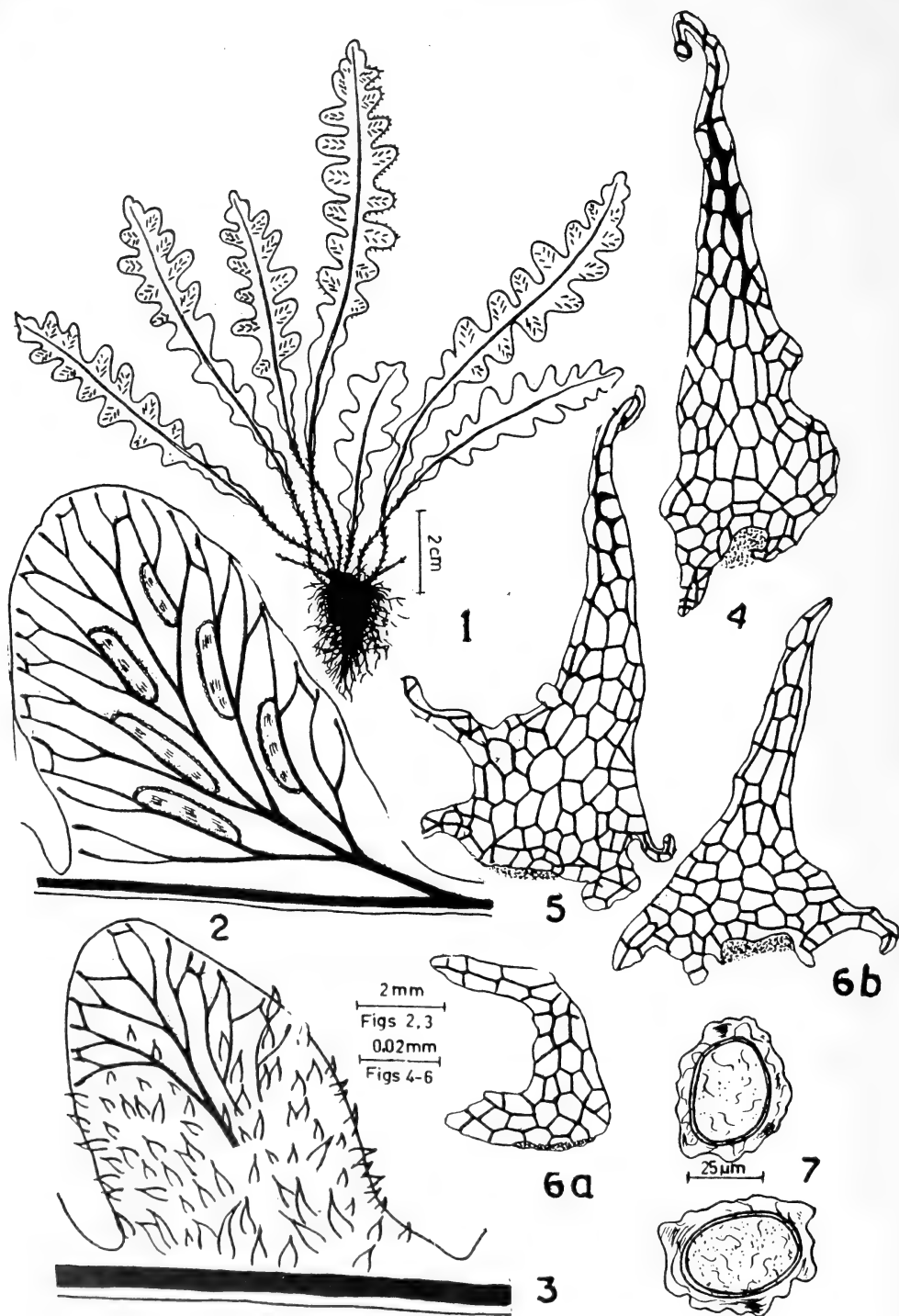
An evergreen plant with its morphology intermediate between *Asplenium dalhousiae* Hooker and *Asplenium ceterach* L. It differs from *A. dalhousiae* by the presence of scales on the abaxial (lower) side of the lamina and by several marginal anastomoses in its venation; it differs from *A. ceterach* in the presence of indusia and by the less dense scale cover on the abaxial side of the lamina. It differs from both species in its larger spores and hexaploid chromosome number with 108 regular pairs of chromosomes (bivalents) at meiosis in sexual reproduction.

Holotype: India (NW Himalaya): Himachal Pradesh, 3km N of Kulu, Beas valley (N of Mandi, N of Simla), 1300m alt., among roadside boulders, growing with *Asplenium dalhousiae*, *A. trichomanes* L. subsp. *quadrivalens* D.E. Meyer and *Pellaea nitidula* (Wall. ex Hook.) Bak. Coll.: C.R. Fraser-Jenkins, 6719, 1/Sept/1977 (PUN no. 3694).

Isotypes: ditto (BM, K).

Paratypes: ditto nos. 6707, 6731 (herb. T. Reichstein, Basel), 6708-6718, 6720-6730, 6732-6735 (PUN, PAN, DD, CAL, RAW, KATH, BM, K, PE, CANU, MICH, US); no. 6733 is also labelled as PUN no. 3693.

A small, perennial evergreen fern. Rhizome upright or shortly ascendent, densely paleate at its apex; scales dark brownish-grey, clathrate, c.4mm long, c. 1mm wide at their base, elongated-triangular in shape with a filiform apex and erose margin; mature fronds 3-15 (-20)cm long, c.0.5-2cm wide, forming a compact tuft of fronds; stipe dark-brown, thin, usually c.1-2cm long, but longer in plants growing in rock crevices, scales at the stipe-base as long as those borne on the rhizome, but becoming smaller further up the stipe and on the rachis; lamina up to 15cm long, linear-



FIGURES 1-7. *Asplenium punjabense*: 1, Habit of plant; 2, Enlargement of pinna lobe showing venation and position of sori; 3, Under side of pinna lobe showing the scales; 4, Scales from rhizome apex; 5, Scale from stipe; 6, a,b, Scales from under surface of pinna lobe; 7, Spores.

lanceolate, pinnatifid or nearly pinnate with deep, ± rounded sinuses between the lobes or segments (pinnae), greyish-green or brownish-green, glabrous on the adaxial (upper) side with a few small scales on the rachis, ± densely covered with clathrate, brownish, acuminate, erose-margined scales, 0.5-2mm in length on the abaxial (lower) side but these do not usually cover the sori completely; the lamina texture is herbaceous to subcoriaceous; segments alternate, ovate to oblong, with the margins somewhat parallel and obtuse apices; venation forked, subflabellate, with the veins partly free and partly anastomosing near the segment margins; sori linear, up to 3mm long, slightly hidden by scales, bearing indusia of the same shape and size as the sorus and c.0.3mm wide; spores monolete with the exospore c.42-50µm long, perispore wrinkled, irregularly protruding from the exospore by up to 10µm as seen in equatorial view. Cytotype: Hexaploid sexual, with 108 regular pairs at meiosis, n = 108. (Figs. 1-7).

Habitat: Apparently without specific soil requirements, on rocks in crevices, or between boulders, also along road sides.

Distribution: Endemic to the Western Himalaya, so far known from the Beas (Kulu) valley in Himachal Pradesh, westwards to Kashmir and NW Pakistan (Swat) at altitudes from 900 to c. 1,800m.

Although very closely resembling *A. ceterach* in habit and frond form, the new spleenwort also shows some similarity to *A. dalhousiae*. But in spite of its intermediate morphology this fern can be distinguished by the combination of features tabulated below:

	<i>Asplenium dalhousiae</i>	<i>A. punjabense</i>	<i>A. ceterach</i> subsp. <i>ceterach</i>
1. Scales on the abaxial side of lamina	absent	moderately dense	very dense
2. Venation	free	partially free	many veinlet fusions
3. Indusium	present	present	absent
4. Spore size (exospore length)	c.28-32µm	c.42-50µm	c.36-45µm
5. Cytotype	n = 36 (diploid)	n = 108 (hexaploid)	n = 72 (tetraploid)

Specimens examined

Asplenium punjabense

(1) *C.R. Fraser-Jenkins* 7871-7888 (18 plants). NW Pakistan: Distr. Swat, lower Swat valley, c. 5km NE of Mingora, N of Saidu Sharif, 950m alt., 1/Oct/1978, stream on shale cliff together with *Pteris vittata* L., *Adiantum capillus-veneris* L., and *Cheilanthes pteridioides* (Reichb.) C.Chr. (all in BM except 7886 given to T. Reichstein).

(2) *C.R. Fraser-Jenkins* 7894-7904, NW Pakistan: Distr. Swat, mid Swat valley, c. 4km S of Madyan, N of Saidu Sharif, 1,300m. 1/Oct/1978, below boulders at road side together with *Pteris cretica* L., *Dryopteris nigropaleacea* (Fras.-Jenk.) Fras.-Jenk., *Asplenium trichomanes* L. subsp. *quadrivalens* D.E. Meyer and *Pellaea nitidula* (Wall. ex Hook.) Bak. (all in BM except 7895 and 7902 given to T. Reichstein, 7901 in PE).

(3) *S.P. Khullar* 244, Kishtwar (Kashmir). Alt. 1,700m. Grows on open dry slopes, rare. July/1980 (PUN 3644), with *A. ceterach* and *A. dalhousiae*.

(4) NW Pakistan: Kulalai Swat, 1,800m. *Muqarrab Shah & Dilawar*, 377 (ISL); Pir Baba, Swat. *Muqarrab Shah & Dilawar*, 1704 (ISL); Karahar, Swat, 1,290m. *Muqarrab Shah & Dilawar*, 122 (ISL); Kedam, Swat, 1,380m. *Muqarrab Shah & Dilawar*, 630 (ISL); Manglor, Swat, 1,100m. *Muqarrab Shah & Dilawar*, 543 (ISL); Bildgram, Swat, 900m. *Muqarrab Shah & Dilawar*, 507 (ISL); Sangota, Swat. *Muqarrab Shah & Dilawar*, 1137 (ISL); Madyan, Swat. *A. Rahman & R.R. Stewart*, 15/Aug/1952 (LAH); Dir, 1,410m. *A. Rahman*, 13/July/1956 (LAH); Swat Ellum, Swat, 1,200m. *Muqarrab Shah & Dilawar*, 28, 18/April/1976, pro parte (ISL).

A. dalhousiae and *A. ceterach* were also collected by Fraser-Jenkins near to the localities for *A. punjabense* in the Swat valley, and *A. ceterach* also occurs in the Beas valley (as well as *A. dalhousiae* mentioned above).

One specimen found growing with the population of *A. punjabense* in the Beas valley has abortive spores and its morphology is clearly and recognisably intermediate between *A. punjabense* and *A. dalhousiae*. This is therefore described as a new hybrid as follows:

Asplenium × *geni-coalitum* Fraser-Jenkins, hybr. nov. (= *A. dalhousiae* × *A. punjabense*).

Planta morphologia intermedia inter *A. dalhousiae* et *A. punjabense*, parum plus paleacea ad paginam abaxialam quam in *A. dalhousiae*. Sporae abortivae.

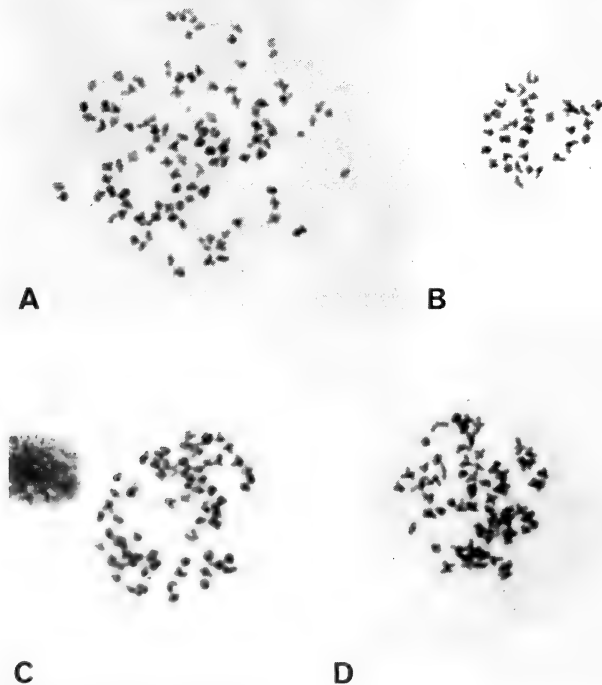


FIGURE 9. Diakinesis in spore mother cells, Xc. 700. Preparations by J.D.L., all from plants grown at the University of Leeds from spores. A, *Asplenium punjabense*, Kulu valley, Bir s.n. (spontaneous), n = 108. B, *A. capense*, Basutoland, leg. A.F. Braithwaite (AB 28), n = 36 (Phase contrast). C, *A. phillipsianum*, Socotra, Gwynne 173, n = ca. 72. D, *A. haughtonii*, St. Helena, Kerr 79, n = ca. 72.

Holotype: Same locality, date and collector as the holotype of *A. punjabense*; no. 6729 (BM). Cytology unknown.

This hybrid is named in recognition of its presumably containing genomes from *Ceterach* and *Ceterachopsis* (as is also true of *A. punjabense*).

DISCUSSION

The taxonomic problems associated with a decision as to the correct systematic treatment of *Asplenium punjabense* are two-fold and individually complex to a degree which renders it unsurprising that the three authors of this paper at first found it difficult to reach agreement regarding the best solution.

There is firstly the question of the relationships of *Asplenium*, *Ceterach* and *Ceterachopsis*. These three groups may be separated primarily on characters of the indusium and frond shape, supported by scale and venation characters. As is illustrated in Fig. 8, there are four tenable treatments recognising all three groups as genus or subgenus. At one extreme (A), each is recognised as a separate genus; at the other extreme (D), ultimately chosen here, both *Ceterachopsis* and *Ceterach* are subordinated to *Asplenium* as subgenera. The situation of *Ceterachopsis* is plainly intermediate between *Asplenium* and *Ceterach* and can with reason, if both these are supported as genera, be treated either as a subgenus of *Asplenium* (C), or as a subgenus of *Ceterach* (D), depending on whether presence/absence of the indusium or frond-shape is granted the greater significance. A more drastic treatment (F), already in effect adopted by Christensen (1905-06), is to recognise *Asplenium* and *Ceterach*, but to submerge *Ceterachopsis* completely within *Ceterach*, granting it no status.

The second question is that of the proper allocation of *A. punjabense*. Its placement, on morphological criteria, is clearly with *Ceterachopsis*, so long as this group is recognised. However, if our hypothesis regarding the ancestral origin of *punjabense* is correct, then it possesses a majority of genomes from *Ceterach*, in a ratio of 2:1 *Ceterach*-*Ceterachopsis*, and is thus logically, in genetic terms, more *Ceterach* than *Ceterachopsis*!* An instructive parallel here is the relationship of *Aegilops* and *Triticum*. Contemporary opinion mostly accepts that hexaploid wheat, *Triticum aestivum*, contains one genome (A) from *Triticum monococcum* and two genomes (B and D) from species of *Aegilops*. Stebbins (1956, p. 238) pointed out that on this basis we "... reach the conclusion that the only 'pure' species of *Triticum*, i.e. which does not contain chromosomes derived from *Aegilops*, is *T. monococcum* ... and the maintenance of *Triticum* and *Aegilops* as separate genera becomes an absurdity". Consequently, most recent authors (e.g. Feldman 1976) submerge *Aegilops* within *Triticum*.

Other "intergeneric" allopolyploid species are known in the Aspleniaceae. These are *Ceterophyllitis hybrida* (Milde) Pich.-Serm. (= *Phyllitopsis hybrida* (Milde) Reichstein, *Phyllitis hybrida* (Milde) C.Chr., *Ceterach reichardtii* Haracic (Vida 1963, Meyer 1981)), *Asplenium castaneo-viride* Bak. (= *A. kobayashii* Tag., *fide* Ching & Iwatsuki 1982 (see Lovis, Brownsey, Sleep & Shivas 1973)), *Asplenium ebenoides* Scott and *Asplenium pinnatifidum* Nutt. (see Lovis 1973, 1977 for review and earlier references). For these species independent generic names (*Ceterophyllitis* Pich.-Serm. and *Asplenosorus* Wherry) are available. We are unanimous in rejecting such a solution for placement of *Asplenium punjabense*. Such a new compound genus would be impossible to characterise satisfactorily.

*The very close morphological affinity between *Asplenium ceterach* subsp. *bivalens* (2x) and *A. ceterach* subsp. *ceterach* (4x) leaves little room for doubt that the tetraploid taxon is either an autotetraploid or of segmental allopolyploid origin from closely related parents — thus all genomes in *A. ceterach* subsp. *ceterach* must be from *Ceterach*.

There can be little doubt that *Ceterach* has evolved from a source in *Asplenium* by changes involving acquisition of scales and a corresponding loss of the (then superfluous) indusium, and that, as indicated by Copeland (1947) and Bir (1963) the source of *Ceterach* must be sought in *Ceterachopsis*. Indeed, our observations support this concept in as much as the indusium is expressed in *A. punjabense*, despite the postulate that it includes four chromosome sets from the ex-indusiate *Ceterach*. This suggests that in *Ceterach* the indusium is still latent and is indeed suppressed. Of course, though *punjabense* reflects a likely intermediate stage in the evolution of *Ceterach* from the vicinity of *Asplenium dalhousiae*, it is not itself literally that intermediate stage. Its hexaploid chromosome number renders that impossible, since it is clear that the evolution of *Ceterach* from *Asplenium* took place at the diploid level. It might be an autohexaploid derivative of some undiscovered or extinct diploid, but the circumstantial evidence, as we have stressed, makes an allopolyploid origin for *punjabense* much more probable.

If, as seems almost incontrovertible, *Asplenium* → *Ceterachopsis* → *Ceterach* constitutes a genuine evolutionary sequence, an interesting conclusion emerges in terms of the scales and indusia — to combine *Ceterachopsis* with *Asplenium* or with *Ceterach* are both equally natural groupings! It is not unnatural to separate in different (but systematically related) taxa two groups that are phylogenetically related, if the segregated group constitutes a discrete intact evolutionary unit. The question as to whether to recognise and how to relate these groups in a systematic scheme is one that has to be resolved on taxonomic and genetical grounds. Fraser-Jenkins would in this particular and somewhat special case of *Ceterach* and *Ceterachopsis* v. *Asplenium* attach greater significance to the frond shape, in which case *Ceterach* and *Ceterachopsis* would become more closely grouped together, which is not able to be reflected in our choice of ranks when both are subordinated to *Asplenium*, as here.

Although the affinity between *Ceterach* and *Ceterachopsis* is self-evident, the source of *Ceterachopsis* within *Asplenium sensu stricto* is not at all clear, and it is evident that subordination of *Ceterachopsis* alone to *Asplenium* (C & E), though taxonomically defensible is, in terms of closeness of relationship, less satisfactory than subordination of *Ceterachopsis* alone to *Ceterach* (B & F), as advocated by Fraser-Jenkins when *Ceterach* is recognised as a genus. However, in the opinion of all three authors, *Ceterachopsis* is a useful concept and should be retained, although only at subgeneric rank within *Asplenium*, bearing in mind that we also subordinate *Ceterach* to *Asplenium*.

There is no doubt that the presence of inter-generic hybrids is an anachronism, and ought to be avoided whenever possible. Lovis (1973) compared the situation in the Aspleniaceae with that in the Orchidaceae and Gramineae in as much as in all three ill-defined generic limits are a consequence of incomplete and recent active evolution. However, in practical taxonomic terms, these cases are not really similar. To disallow intergeneric hybrids in the Orchidaceae and Gramineae would generate drastic changes and produce an inconvenient and possibly unworkable taxonomy with several vast genera, but the Aspleniaceae is already dominated by the huge genus *Asplenium*, and absorption of all its satellite genera back into *Asplenium* has relatively little effect in terms of practical taxonomy.

This is a strong argument against accepting *Camptosorus*, *Ceterach*, *Phyllitis* etc. as independent genera. However these entities, together with *Ceterachopsis*, are useful names for employment in phylogenetic and biosystematic discussion. We have therefore in this paper, for convenience and simplicity, unanimously decided to treat both *Ceterach* and *Ceterachopsis* as subgenera of *Asplenium* in order to preserve them, a treatment already accepted and preferred by Bir (1962, 1963, in Mehra & Bir

1964) for *Ceterachopsis*, and proposed, but not formally adopted, for *Ceterach* by Vida (1963) and Lovis & Vida (1969). Fraser-Jenkins strongly advocates though that when *Ceterach* is treated as a genus it is better to treat *Ceterachopsis* as a subgenus of it.

SYSTEMATIC SYNOPSIS

The new grouping of species is as follows:

Asplenium:

- (a) Subgenus *Ceterachopsis* (J. Smith ex Ching) Bir in Mehra & Bir, Res. Bull. Panjab. Univ., N.S., 15: 159 (1964).
 1. *Asplenium dalhousiae* Hook., Icon. Plant.: t. 105 (1837). Type species of the subgenus (*Ceterach dalhousiae* (Hook.) C. Chr., Ind. Fil. 1: 170 (1905); *Ceterachopsis dalhousiae* (Hook.) Ching, Bull. Fan Mem. Inst. Biol., Bot. Ser., 10: 1-22 (1940); *Asplenium alternans* Wall. ex Hook., Sp. Fil. 3: 92 (1860)). (Diploid, $2n = 72$).
 2. *A. paucivenosum* (Ching) Bir, Bull. Bot. Surv. India 4: 3 (1962) (*Ceterach paucivenosa* Ching, Bull. Fan Mem. Inst. Biol., 2: 210, t. 28 (1931); *Ceterachopsis paucivenosa* (Ching) Ching, Bull. Fan Mem. Inst. Biol., Bot. ser., 10: 1-22 (1940); *A. paucivenosum* forma *minus* Bir, Amer. Fern J. 62: 46 (1972)). (Tetraploid, $2n = 144$. See Bir 1962, 1972).
 3. *A. punjabense* Bir, Fraser-Jenkins & Lovis. (Hexaploid, $n = 108$).
 4. **A. birii** (Löve & Löve) Bir, Fraser-Jenkins & Lovis, **comb. nov.** *Asplenium paucivenosum* f. *majus* Bir, Amer. Fern J. 62: 46 (1972); *Ceterachopsis birii* Löve & Löve in Taxon 26: 326 (1977). (Octoploid, $2n = 288$). The relationship of this species to *A. magnificum* (Ching) Bir, Fraser-Jenkins & Lovis requires further study.
 5. **A. magnificum** (Ching) Bir, Fraser-Jenkins & Lovis, **comb. nov.** (*Ceterachopsis magnifica* Ching, Bull. Fan Mem. Inst. Biol., Bot. Ser., 11: 56 (1941)). (Cytology unknown).
 6. A sixth taxon from China has recently been named in the herbarium at Peking as *Ceterachopsis latiloba* Ching & Shing, ined. and appears to be a distinct species requiring further study.
- (b) Subgenus *Ceterach* (Willd.) Vida ex Bir, Fraser-Jenkins & Lovis, **stat. nov.** (*Ceterach* Willd., Anleit. Selsbstud. Bot.: 578 (1804), *nom. cons.*).
 1. *Asplenium ceterach* L. Sp. Plant. 2: 1080 (1753). Type species of the subgenus (*Ceterach officinarum* DC in Lam. & DC., Fl. Franc. 2: 566 (1805)).
 - a. Subsp. *ceterach*. (Tetraploid, $2n = 144$).
 - b. Subsp. *bivalens* (D.E. Meyer) Greuter & Burdet, Willdenowia 10: 17 (1980).
(*Ceterach officinarum* subsp. *bivalens* D.E. Meyer, Ber. Deutsch. Bot. Ges. 77: 8 (1964); *Asplenium javorkeanum* Vida, Acta Bot. Acad. Sci. Hung. 9: 202 (1963)). (Diploid, $2n = 72$).
 2. *Asplenium aureum* Cav., Anal. Cienc. 4: 100 (1801); Descr. 256 (1802) (*Ceterach aureum* (Cav.) L. v. Buch., Abh. Akad. Wiss. Berlin 1816-17: 361 (1819). See Benl & Kunkel (1972)). (Tetraploid, $n = 72$ (Canaries); hexaploid, $n = 108$ (Madeira); octoploid, $n = 144$ (Canaries)). Evidently a complex requiring further taxonomic and cytogenetic study.
 3. **Asplenium capense** (Kze.) Bir, Fraser-Jenkins & Lovis, **comb. nov.** (*Ceterach capensis* Kze. Linnaea 10: 496 (1836)). (Diploid, $n = 36$; Braithwaite 28, BM. Chase 6822, Umtali, S. Rhodesia (Zimbabwe) is tetraploid, $n = c. 72$. Morphologically this collection fits better with this

species than with *cordatum* Sw.). Clearly the *capense/cordatum* group also requires further study.

4. *Asplenium cordatum* Sw., Schrad. J. Bot. 1800: 54 (1801) (*Acrostichum cordatum* Thbg, Prod. Fl. Cap.: 171 (1800); *Ceterach cordatum* (Thbg) Desv., Prod.: 223 (1827)). (Tetraploid, $n = c. 72$; Braithwaite 141, BM).
5. *Asplenium haughtonii* (Hk.) Bir, Fraser-Jenkins & Lovis, **comb. nov.** (*Gymnogramme haughtonii* Hk. in Hooker & Baker Synopsis Filicum 381 (1868)). (Tetraploid, $n = 72$; St. Helena, Kerr 79).
6. *Asplenium phillipsianum* (Kümmerle) Bir, Fraser-Jenkins & Lovis **comb. nov.** (*Ceterach phillipsianum* Kümmerle Botan. Közl. 6: 287 (1909); Mag. Bot. Lap. 8: 354 (1909)). (Tetraploid, $n = 72$; Socotra, Gwynne 173, BM). (This species requires further study in order to circumscribe the diagnostic features distinguishing it from *A. ceterach* subsp. *ceterach*.)

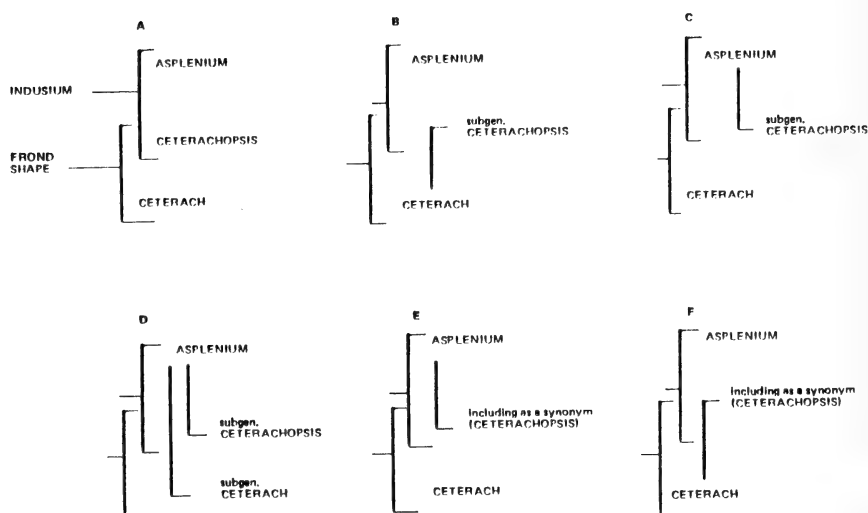


FIGURE 8. Systematic relationship of *Asplenium*, *Ceterachopsis* and *Ceterach*. Six alternative treatments: A, Three separate genera; B & C, *Ceterachopsis* treated as a subgenus of *Ceterach* (B) or *Asplenium* (C); D, Both *Ceterachopsis* and *Ceterach* treated as subgenera of *Asplenium*; E & F, *Ceterachopsis* not recognised, submerged into either *Asplenium* (E) or *Ceterach* (F).

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THE MODULAR GROWTH OF *LYCOPODIUM ANNOTINUM*

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ABSTRACT

Lycopodium annotinum L. is a long-lived plant which consists of a series of annually produced segments which can be aged. This paper describes in detail the modular construction of the plant and analyses elements of deterministic and opportunistic growth by synthesizing a 20-year life cycle from historical records of the plant's growth.

By regarding a plant as a population of modules it is possible to use the methods of population biologists for discontinuous variables and the approach of growth analysis when studying continuous variables.

The balance between deterministic and opportunistic growth produces a foraging behaviour which enables the plant to harvest patchy resources, and to escape interspecific and intraclonal competition. The survival of the plant in its unfertile yet relatively predictable environment is enhanced by the recycling of nutrients between senescing tissues and growing points. This results in indefinite growth and the dominance of vegetative proliferation. Opportunistic colonization of new habitats is possible through the subsidized growth of pioneering horizontal modules and a constant production of airborne propagules which colonize open habitats outside existing locations. "Opportunistic escape" occurs when environmental adversity, such as hard substrate or prevented root formation, kills dominant growing points resulting in lateral branch proliferation and a great extension of the potential zone of exploitation.

The result is a plant which is successful in both colonizing and surviving in a spatially and temporally heterogeneous habitat.

INTRODUCTION

The sporophyte of *Lycopodium annotinum* L. (Interrupted Club-moss) is a particularly useful tool for investigating population processes and modular growth due to its construction of repeated units (segments) within horizontal and vertical branches (modules). Seasonality in climate produces markers of annual growth (Callaghan & Collins 1976) which allow a plant to be divided into a series of annually produced units which, in cold climates, persist for a long time after death due to slow decomposition rates (Jenny et al. 1949). Roots and strobili can also be regarded as segments and, as the plant is long-lived, a time-specific investigation can yield data on growth, demography and physiology for a period of over 20 years.

The advantage of describing a plant as a population of defineable units (Prévost 1978; White 1979, 1984; Harper 1981) is that the methods used by population biologists are available. The growth of a plant can then be described in terms of numbers of units, the growth of these units and their death, survival and fecundity (Kays & Harper 1974; Callaghan 1976, 1984; Bazzaz & Harper 1977; Maillette 1982; McGraw & Antonovics 1983).

It is also possible to interpret interactions between the environment and growth, development and physiology of the repeated units in the long term context of the population of units within the whole plant (Callaghan 1984; Headley et al. 1985; Callaghan et al. 1986).

Populations of repeated growth units may be studied either by determining age class distributions and assuming a stable population to calculate rates of survival (Kawano et al. 1982) or by following a cohort throughout its life cycle (Deevey 1947; Merrell 1947; Harper 1967). The first method fails if the population is unstable (Callaghan & Emanuelsson 1985) whereas the second method is impractical with long-lived perennials. *Lycopodium annotinum* presents a plant in which patterns of survival can be recorded for a past period by identifying the dates and ages at which module death occurs.

This paper describes in detail the modular growth (or metameric growth, sensu White 1984) of this long-lived plant from a stressed environment. The paper serves as a basis for detailed investigations of the interactions between the plant and its micro-environment (Svensson & Callaghan unpubl.) and long-term age-based physiological processes (Headley et al. 1985; Callaghan et al. 1986).

MATERIALS AND METHODS

The study was carried out at the Abisko Scientific Research Station on the south shore of Lake Torneträsk in Swedish Lapland (68°23'N, 18°55'E). The site was situated in the boreal birch forest and was dominated by low density *Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman and the ground vegetation consisted mainly of *Vaccinium vitis-idaea* L., *V. uliginosum* L., *Empetrum hermaphroditum* Hagerup, *Linnaea borealis* L., and *Hylocomium splendens* B. & S. Climatic and micro-climatic characteristics of the site together with a more detailed description of the vegetation are presented in Callaghan et al. (1978) under the heading "*Hylocomium* site".

Observations were made in three years: 1975, 1980, and 1982. During 1975, 71 plants were excavated carefully in the field by tracing the prostrate stems back to a point where they were decomposing and their integrity had been destroyed. The plants were pressed dry and returned to the laboratory for analysis. In 1980 and 1982, two areas of vegetation 3.8 × 4.2m were mapped in detail, including the exact positions of all the horizontal modules of *L. annotinum*. The plants were then excavated, and after measuring the length of each annual increment, and the location of each root, the plants were pressed dry for further analysis.

In the laboratory, each plant was divided into its component segments and the age of each was determined by counting successive morphological markers of annual growth (see Callaghan 1980). The relationship between every annual segment within a plant was recorded, as well as dry weight, and number of daughter segments. It was also recorded if the segments were dead (i.e. brown with detached microphylls) or alive. Of the individual segments analysed in 1975, 1980, and 1982, data from approximately 15,000 are presented here.

Correlations between mean monthly temperatures and annual growth were made. To reduce the effect of length variations between segments resulting from differences in module size, segment lengths were converted to a length index (I) using a method described by Fritts (1976). Variation between segments within modules due to positional effects was reduced by omitting the small first segment within each module from the analyses, although regressions were not required to remove further variation (Fritts 1976) as recognizable trends of segment length within modules were absent. The length index I was calculated as $I = L_m / B_e$ where L_m is the measured length of a segment and B_e is the expected segment length estimated as mean segment length per module.

RESULTS

Organization of the plant and allocation of dry matter

The sporophyte of *L. annotinum* consists of a series of annually produced segments which are aggregated modules growing apically and senescing distally, as the plant moves across the ground. Arising from the horizontal segments are smaller, vertically orientated photosynthetic segments which are densely covered with microphylls. These vertical segments are aggregated into "vertical modules", which are terminated either by the death of the youngest vertical segment in the module or by the initiation of a spore-producing strobilus (Fig. 1). Horizontal segments may produce other horizontal segments, roots and vertical segments. In contrast, vertical segments can only usually produce other vertical segments and strobili.

The growth of a major plant unit, i.e. a horizontal module (without lateral modules) and all of the vertical modules, strobili and roots attached to it, shows a rapid accumulation of dry weight reaching a maximum of 3.8g in its seventh year (Fig. 2a). Thereafter, weight is lost gradually over a period of more than 17 years.

The survival of the horizontal module is theoretically indefinite (Fig. 1) but the probability of survival of an individual horizontal segment decreases as its age increases, which is a familiar biological pattern.

For the first 2 years, horizontal segments contribute most of the dry weight but vertical modules grow rapidly and are the major contributor of biomass for 10 years with a peak in year 6 (Fig. 2b). Living horizontal segments survive longer than vertical modules and after 13 years horizontal segments are again the major — and ultimately the only — contributor of biomass as the vertical modules decompose and become detached. The probability of survival of vertical segments varies from that described for horizontal segments (Fig. 1) and is described in detail below. Strobili are strictly annual structures and attain dry weights of 18mg (Callaghan 1980).

Roots contribute a maximum of 5% of the total biomass and reproductive effort in terms of dry weight of living strobili reaches only 5.1% of the total biomass (Fig. 2b).

Growth of horizontal modules

Differentiation of segments. When a new horizontal side-module is formed, the first segment to be produced within that module is always smaller in terms of dry weight and length than those subsequently produced. For example, the mean length of the first segment of modules collected in 1980 was 23.4 ± 1.8 (s.e.)mm ($n = 223$) compared with that of other segments which was 68.2 ± 1.7 (s.e.)mm ($n = 558$). The remaining segments show no recognizable differentiation in relation to their order within the module.

Apical dominance. The apex of a main horizontal module of *L. annotinum* is an active and fast growing organ which may photosynthesise (Callaghan 1980). Indeed, it is during the first year of growth when roots, vertical modules and other horizontal segments are formed (Fig. 1). Growth in this year may reach 170mm and 24mg dry weight. This active apex exerts a significant inhibition of the growth of daughter-modules such that the effect increases from the oldest to the youngest lateral module in a relationship described by: $y = 71 - 3.88x$ ($r = 0.64$, $p < .001$, degrees of freedom = 224) where y = length of one year old segment as percentage of one year old segment of dominant branch, and x = order of branch initiation covering 13 orders of dominance (see Fig. 3 of Callaghan & Emanuelsson 1985).

At any one time, the population of apices consists of those surviving from the previous year, recently dead or dying apices, and newly initiated apices. The production of new apical meristems is strongly correlated with the death of dominant apices and varies from year to year (Fig. 3).

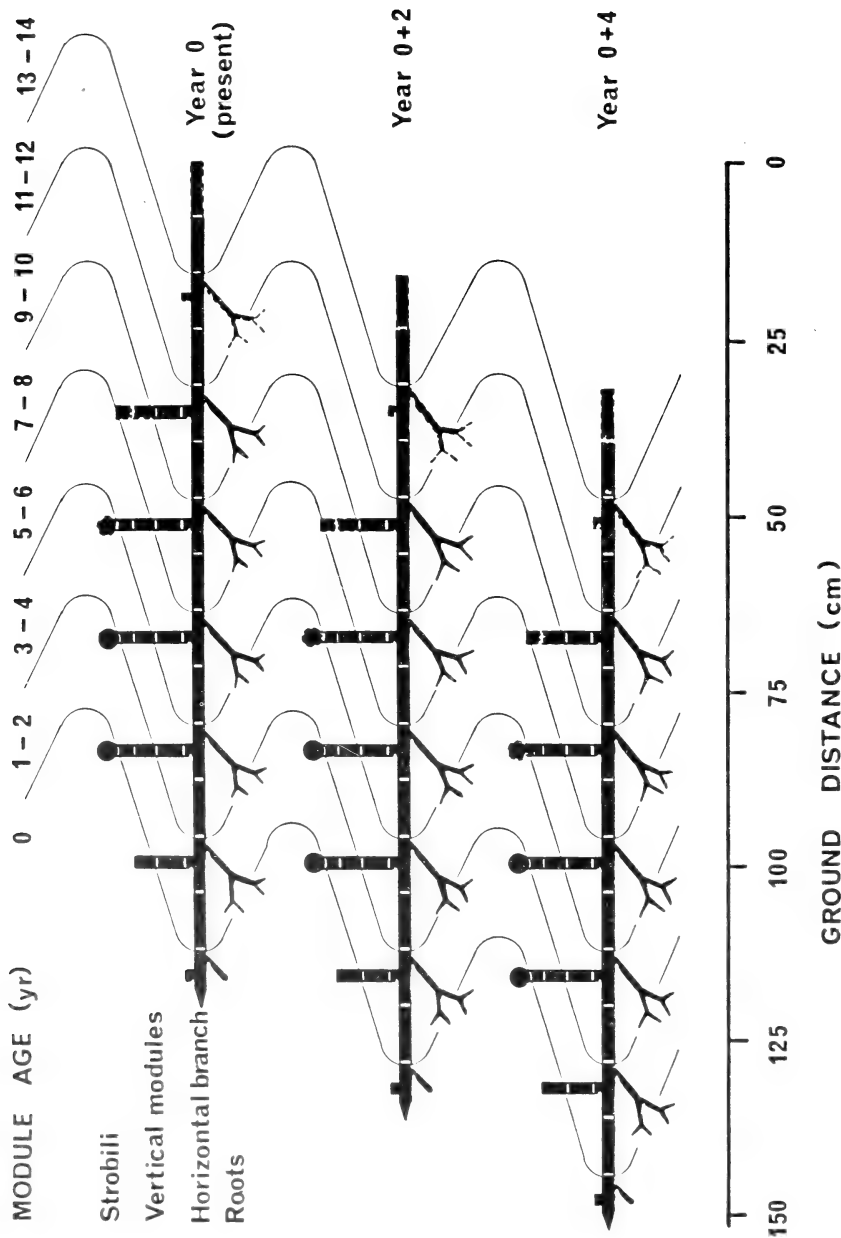


FIGURE 1. Diagrammatic representation of the growth and movement of an unbranched plant of *L. annotinum*: For simplicity vertical modules and roots are shown on alternate horizontal segments. The lighter hatched areas represent senescing tissues whereas the dotted lines contain decomposing tissues also represented by lighter hatching. White breaks represent annual markers of growth while the contours denote age classes for the segments.

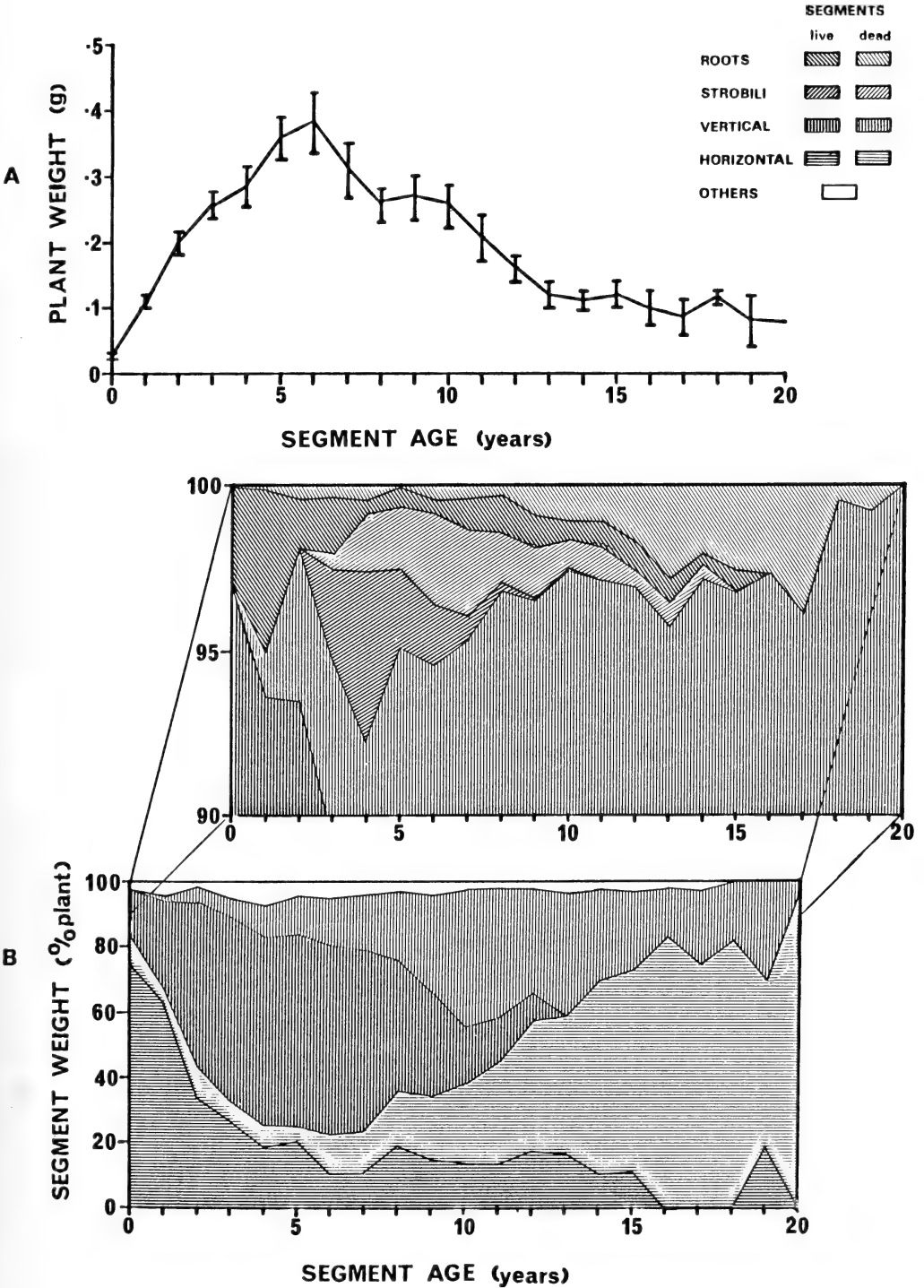


FIGURE 2. The dry weight trends (a) and dry weight partitioning (b) in an unbranched plant of *L. annotinum* over its life cycle. Bars represent standard errors. The data are based on samples collected in 1975 with a sample size of 1079 horizontal segments.



FIGURE 3. The relationship between the initiation of daughter-modules (reproduction, thick line) and the survival of existing horizontal modules (thin line) over a 22 year period. Data are presented for samples collected in 1975, 1980, and 1982. Correlation between annual means: $r = -0.86$ (***) with 21 d.f.).

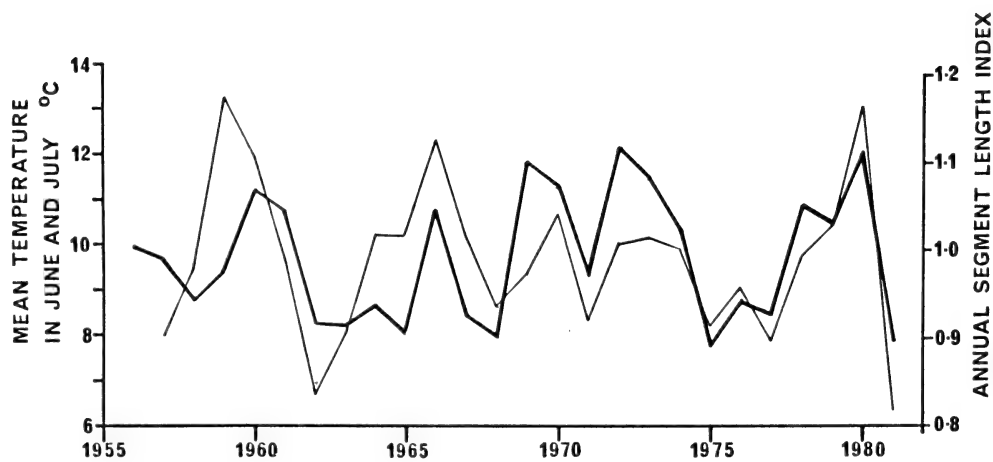


FIGURE 4. The relationship between the index of annual horizontal segment length (thin line) and the mean monthly temperature (thick line) for the summers of the years 1955 to 1981. Data are based on samples collected in 1975, 1980, and 1982 ($n = 1698$). See Table 1 for correlation analysis.

Climate. The final length of an horizontal segment is achieved within its year of initiation and length is therefore a useful variable to correlate with climate.

Relationships between mean monthly temperature and segment length show significant positive correlations for the summer months June and July and particularly for the combination of June plus July (Fig. 4). It would appear that 1975 was a particularly adverse season both for segment extension growth (Fig. 4) and survival (Fig. 3). No correlation was found between survival and precipitation nor between survival and temperature.

Growth of vertical modules

Differentiation of segments. There are great differences of growth between vertical segments according to their roles within the module. The first segment to be produced in a vertical module is the smallest whereas the second is the largest (Fig. 5). Segments produced after the second show a successive decrease in dry weight (Fig. 5). The differentiation mainly results from variations in growth rates during the first season of growth. Relative Growth Rates (RGR) of segments 1 to 3 were .021, .047, and .049g/g/day respectively (the strobilus had a RGR of .056g/g/day over the same period i.e. 17 June to 10 August).

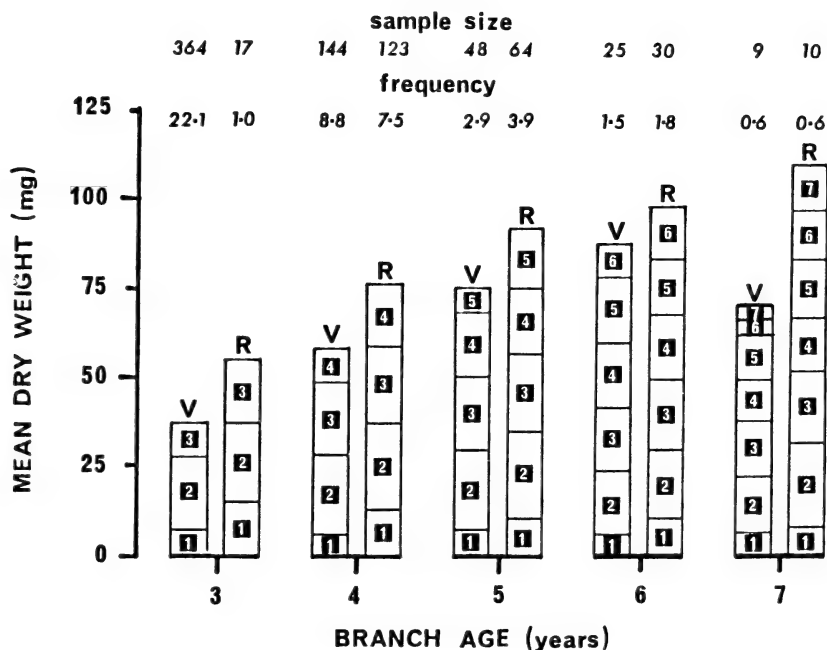


FIGURE 5. Comparison of the dry weights of segments of similar ages and position within vegetative (V) and reproductive (R) vertical modules. Numbers within black bars are the position of the segment within the module. The mean dry weight for segment 1 of vegetative and reproductive modules was 7 (n = 590) and 11.9mg (n = 244) respectively, $t = 7.4$ (***). The mean dry weight of all other segments for vegetative and reproductive modules was 19.8 (n = 941) and 21.4mg (n = 625) respectively ($t = 1.86$ N.S.). t for differences between segments 1 and the remaining segments of vegetative and reproductive modules = 19.5 (***) and 10.8 (***) respectively. Data from samples collected in 1975. The frequency of age classes 1 to 7 of vertical modules (as percentage of 1644) is also given: the frequencies of age classes younger than 3 were 48.8% (vegetative) and 0.06% (reproductive). Those for age classes older than 7 years were 0.7% (vegetative) and 0.42% (reproductive).

TABLE 1. Branching in relation to segment position within reproductive vertical modules, and, strobilus weight in relation to age of reproductive modules (standard errors are given in brackets).

		Size of reproductive module (= numbers of vegetative segments plus strobilus):						
		2	3	4	5	6	7	> 7
Number of modules	1:	0	.294(.117)	.309(.055)	.219(.079)	1.3(.13)	.3(.161)	—
produced per	2:	—	.118(.083)	.423(.057)	.828(.116)	.833(.162)	1.4(.172)	—
vegetative	3:	—	—	.041(.018)	.141(.05)	.467(.117)	.7(.161)	—
segment for	4:	—	—	—	0	.67(.047)	.2(.014)	—
segment	5:	—	—	—	—	0	0	—
positions:	6:	—	—	—	—	—	0	—
strobilus dry weight (mg):		—	17.7(2.6)	17.0(.9)	16.7(1.3)	14.9(2.0)	12.6(3.4)	6.6(2.9)
	no:	1	17	123	64	30	10	5
Sample size:								
	%:	.4	6.8	49.2	25.6	12	4	2

TABLE 2. Comparison between segments on branches with living apices (n = 263) and dead apices (n = 336) of numbers of roots produced (n = 182 and 215, respectively) and the length supported by them. Means \pm standard errors are presented.

	BRANCHES WITH APICES	
	LIVING	DEAD
Length of segment (mm) with:		
0 roots / segment	48.8 \pm 2.6	50.9 \pm 2.2
1 root / segment	71.2 \pm 3.2	71.2 \pm 2.4
2 roots / segment	86.6 \pm 3.2	101.6 \pm 4.9
3 roots / segment	131.0 \pm 22.7	116.8 \pm 10.1
Overall length / segment (mm)	63.5	65.2
Overall length of segments / root (mm)	91.8	101.9
Percentage of segments with:		
0 roots / segment	46.8	50.6
1 root / segment	38.4	36.0
2 roots / segment	13.7	12.2
3 roots / segment	1.1	1.2
Overall number of roots / segment	0.69	0.64
Number of roots / dm ²		0.43
Longest distance between apex and root (mm)		275

Associated with the differentiation of segments is a pattern of proliferation whereby daughter-modules are produced. In all vertical modules, vegetative reproductive capacity is minimal in the last segments to be produced independently of the ultimate size of the module (Tab. 1). In modules with 3 or more vertical segments, branching frequency is greatest in the second and largest module (Tab. 1). However, branching is not associated with size as the smallest segments (the first in a module) form more new segments than larger segments (i.e. the third, fourth etc.).

Production of strobili. The ultimate role of a vertical module is to support a strobilus but strobili may terminate vertical module growth at any stage. Large modules, i.e. those with greater numbers of vertical segments plus a strobilus, are common, and strobilus weight decreases as module size increases. Modules composed of 3 vertical segments and a strobilus clearly show the greatest frequency and largest strobili (Tab. 1).

The population of vertical modules. At a given point in time vertical modules attached to the same horizontal system may survive and remain vegetative, initiate a strobilus, or die. The frequency of strobilus-bearing modules is smaller than that of vegetative modules until age class 5 (Fig. 5). Branches consisting of vertical segments with high dry weights have a greater probability of producing a strobilus and this is even detectable in the small first segments of vegetative and reproductive modules (Fig. 5).

Vertical modules show an inverted pattern of age-based mortality since the first segment to die is the youngest and the last to die is the oldest first segment (Fig. 1). This is the opposite of that seen in horizontal modules.

Spore production

Spore production has been estimated by Plotnikov (1977) as 0.4×10^6 per strobilus and, with a strobilus density of 4.7 per dm^2 (0.23 ± 0.026 (s.e.)) as recorded in the present study, there would be an annual spore production of 1.88×10^6 per dm^2 per year. The viability of spores is low, only 4% (Svensson unpubl.).

Root production

Roots are produced in a very regular way by *L. annotinum*: they are always initiated on year 0 horizontal segments and then grow and branch over a four year period. Thereafter, deterioration is slow but they may still be functional after 13 years (Headley et al. 1985). As the age of the roots increases, the dry weight increases relative to the fresh weight, probably due to suberization (Headley et al. 1985).

At least 1 root is initiated by each horizontal segment but root survival is uncertain so that a mean of 0.69 healthy roots per segment was recorded on healthy modules in which the apex was active (Tab. 2). Only a small percentage of segments possessed 2 or 3 healthy roots (Tab. 2). Root weight only reaches 5% of total plant dry weight which is at the lower end of the range for evergreens (Shaver & Cutler 1979, Miller et al. 1982) (Fig. 2b).

The average length of a horizontal module supported by a root is 91.8mm, and the longest distance found between apex and root was 275mm (Tab. 2).

DISCUSSION

The genus *Lycopodium* is primitive in terms of life cycle, morphology and anatomy, yet highly successful. *Lycopodium annotinum* and some other members of the genus (*L. selago*, *L. complanatum*, *L. clavatum* and *L. alpinum*) are successful even in severe environments and form an important component of upland boreal and tundra vegetation. Their success is based on an ecological strategy enabled by a particular balance between opportunistic and deterministic growth (Tomlinson 1982).

At the first level of organisation, growth of *L. annotinum* is deterministic in that the sporophyte is rigidly organized into a predictable pattern of horizontal modules, vertical modules, roots and strobili.

Horizontal module growth is strongly opportunistic; only the small first segment to be produced in a module shows any rigid genetic control although apical dominance controls the relative size of segments. Climate has a major effect on the actual size of horizontal segments. Survival of the horizontal apex is also opportunistic and is controlled by the ability of roots to function.

Water potential gradients are such that the horizontal apex has the lowest water potential and draws water and nutrients from roots as old as 12 years which may be 1m away (Headley unpubl.). This means that the growth of the apical part of the plant is subsidized and does not necessarily reflect its immediate environmental conditions.

Eventually, however, the subsidized growth of growing points appears to become impossible and they die. This then releases other sub-dominant apices from inhibition and thereby enables a flexible response by increasing the potential range of habitat exploitation (see Callaghan & Emanuelsson 1985, Fig. 6). This selection of apices by the environment helps to control the direction of the plant and when rooting becomes possible, a dominant apex extends the clone in a direction dictated mainly by micro-topography (Svensson & Callaghan unpubl.). Modules with dead apices had fewer roots per cm (Tab. 2) while the horizontal apex has been shown to have depressed water potentials on root excision or increased distance from the nearest viable root (Headley unpubl.). This lends some support to the hypothesis that a major cause of apical death is the inability of roots to grow.

The proliferation following apical death is most often a response to the micro-environment as correlations with climate were not significant. The result is opportunistic escape from this unsuitable microenvironment (Tomlinson 1982) and may be likened to the foraging behaviour of an animal. It may be argued that the "foraging" behaviour of *L. annotinum* is a successful strategy in a heterogeneous environment but that, when favourable microhabitats are found, the plant is at a disadvantage since it must grow away from them. However, if *L. annotinum* remained in such favourable microhabitats it would soon be over-grown by competitive plants, such as the different ericaceous species (Svensson unpubl.). The foraging behaviour is therefore successful in a heterogeneous environment and also avoids competition.

The growth of vertical module segments, in contrast to that of horizontal modules, is deterministic. It is possible to predict which vertical segments will be terminated with a strobilus and which will remain vegetative while the production of daughter modules from the second vertical segment is regular. However, module size (i.e. the number of segments, including strobilus) is not predictable. Vertical modules initiated in the same year may carry strobili in different years. The decreasing size of the strobilus in relation to increasing module size and height may be related to the increasing costs of translocation of nutrients and water (Wallén 1983), and/or the lack of support tissues in this "primitive plant".

Perennials show a small allocation of dry weight to sexual reproduction compared with annuals and biennials. In *L. annotinum*, this allocation reaches a maximum of 5.1% of dry weight which is similar to values quoted by Chester and Shaver (1982) for evergreen and deciduous plants from Alaska and to tundra plants in general (Callaghan and Emanuelsson 1985). The probability of successful reproduction is reduced even further by a low spore viability of only 4%. However, low spore viability and the small allocation of dry matter are compensated for by the vast number of spores produced by a strobilus (0.4×10^6) and the considerable longevity of reproducing clones of up to 250 years (Oinonen 1968). During 250 years, a clone may produce 1.5×10^{14} spores (Callaghan & Emanuelsson 1985). Successful reproduction from spores is probably related to the opportunistic colonization of disturbed areas as in *Viola* (Newell 1983).

The death of the apical parts of vertical modules before that of the lower segments, together with the greater longevity of the horizontal segments, allows the retranslocation of elements from senescing vertical segments into the horizontal axis and subsequently to new growing points. This transport may be between 63 and 90% efficient in terms of N, P and K (Callaghan 1980). Also, translocation of ^{14}C (Callaghan 1980) was found to be extensive, as in stoloniferous *Viola blanda* (Newell 1982). Such efficient translocation allows the subsidized exploratory growth of the main axis when obstacles are encountered. However, should the obstacles be unsurmountable to the main axis, there is a flexible and opportunistic response whereby lateral axes are initiated and released from suppression with a consequent greatly enhanced zone of exploitation.

In conclusion, the sporophyte of *L. annotinum* shows a balance between deterministic and opportunistic growth which

- 1) enables the plant to harvest patchy resources from a spatially heterogeneous environment via a foraging strategy,
- 2) reduces competition within the clone by controlling branching patterns,
- 3) reduces competition with other species by producing roots and vertical modules in available niches along a constantly advancing axis,
- 4) allows survival in impoverished soils by recycling nutrients between segments,
- 5) enables varying degrees of environmental adversity to be overcome first by subsidized growth and then by opportunistic escape following lateral module proliferation,
- 6) allows survival in a temporally predictable environment by indefinite growth associated with vegetative reproduction, and,
- 7) enables opportunistic colonization outside existing locations (e.g. following forest fires) by constant production of vast numbers of airborne propagules.

It is not surprising therefore, that this primitive plant is so important ecologically throughout the northern latitudes.

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THE ECOLOGY OF PTERIDOPHYTES IN TASMANIAN COOL TEMPERATE RAINFOREST

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ABSTRACT

Forty nine pteridophytes from 17 families are reported from cool temperate rainforest in Tasmania. Epiphytes and terrestrial species are both well represented. Their occurrence is influenced by altitude and forest type, but on a regional basis most species are widespread. The biogeographical affinities of the rainforest fern flora are with New Zealand and southern parts of the eastern Australian mainland.

INTRODUCTION

The fern flora of Australia is considered small in relation to the area and latitude of the continent (Page & Clifford 1981), containing about 416 species in 118 genera (Jones & Clemesha 1981). Only four genera are endemic to Australia (all non-Tasmanian) and although six others have a predominantly southern hemisphere distribution most are widely dispersed on a global basis. Within Australia, the ferns attain their greatest richness in Queensland in tropical rainforests and cloud forests. Generic diversity decreases southwards towards Tasmania and also westwards from the coast to the drier parts of the continent (Page & Clifford 1981).

Within Tasmania, ferns and their allies are common but they show no pronounced specialisation to the Tasmanian environment with only two of approximately 90 species being endemic. The group is widespread in the state, occurring in most vegetation types but reaching its greatest diversity in rainforest, wet sclerophyll forest and moist gullies in drier areas. According to Page & Clifford (1981), the number of individuals in temperate rainforest and fern gullies in Tasmania and Victoria is very striking but their diversity is much lower than could be expected from analogous situations in the tropics. Furthermore, they comment that "almost every dominant species seems to have a much wider ecological range than its tropical counterpart, and consequently most occur virtually everywhere that appropriately moist forests and fern gullies are present".

Although the composition of Tasmania's fern flora is well-known (apart from a few taxonomic uncertainties), publications which deal directly with the ecology and distribution of species are scarce. This publication comprises an account of the ferns in Tasmanian cool temperate rainforest and is based mainly on information obtained during a broader examination of rainforest in Tasmania (see Jarman et al. 1984).

METHODS

The Environment — Cool Temperate Rainforest

Tasmania is a mountainous island situated approximately 240 km south of the south-eastern corner of mainland Australia, between latitudes 40° and 43°S. Its rainforest vegetation is classified as cool temperate rainforest and forms part of the island's Antarctic element (after Hooker 1860) or relict sub-element (after Nelson 1981).

Rainforest in Tasmania is defined as forests greater than 8 m tall, dominated by *Nothofagus*, *Eucriphia*, *Phyllocladus*, *Athrotaxis*, *Lagarostrobos* or *Diselma* (Jarman & Brown 1983). It is widespread in the western half of the state with the largest unbroken tracts occurring in the northwest. Smaller patches of rainforest occur also in the northeast, with isolated pockets scattered elsewhere in the eastern half of the

state, usually in gullies. It occurs on both mineral and organic soils, and overlies a wide range of rock types from basalts, dolerite and granite to quartzites and sandstones. The rainfall requirements of rainforest in Tasmania have been given by Jackson (1968) as 1000mm per annum with a summer monthly minimum of 25mm. Rainforest extends from sea level to over 1200m in altitude.

On the basis of floristic and structural characteristics, rainforest has been divided into four groups (Jarman et al. 1984). Group I (Callidendrous rainforest) is characterised by parklike forests with open understoreys, often with a layer of tree ferns. The main canopy trees are *Nothofagus* and *Atherosperma*, and the diversity of woody species in the forest is low. Group II (Thamnic rainforest) also includes forests with well-formed trees but they rarely appear parklike because of a shrubby understorey. The diversity of woody species is higher than in Group I and the main canopy trees are *Nothofagus*, *Atherosperma*, *Eucryphia lucida*, *Phyllocladus*, *Lagarostrobos* and/or *Athrotaxis selaginoides*. Group III (Implicate rainforest) is of lower stature and the trees are often of poor form. The understorey is dense with a tangled shrub layer from ground level to the canopy. Diversity of woody species is high. The main canopy dominants include *Phyllocladus*, *Athrotaxis*, *Eucryphia* and *Nothofagus*, but *Leptospermum* and *Acacia* species may also be present. Group IV (Open montane forest) is dominated by *Athrotaxis cupressoides* and comprises low open forests over grassy or low shrubby understoreys, the latter usually being less than half the height of the forest. The first three groups form the bulk of rainforest in Tasmania and they occur from lowland to highland areas. Thamnic and implicate rainforest reach their best development in western and southwestern Tasmania whereas callidendrous rainforest is best developed in northwestern, central and northeastern Tasmania. Open montane rainforest is confined to high altitudes and is found mostly on the Central Plateau.

Sampling

The survey of pteridophytes was part of a broader survey of rainforest in Tasmania (Jarman et al. 1984) involving both phanerogams and cryptogams. Cover and abundance data were collected from over 300 quadrats (20 × 20m) which sampled the broad geographic and altitudinal range of rainforest throughout the state. Supplementary data were used from Jarman and Crowden (1978). General comments relating to the occurrence of ferns in vegetation other than rainforest are derived from literature sources where indicated, from herbarium records or from unpublished observations.

"Mixed forest" (a rainforest understorey below eucalypts — see Gilbert 1959) was not systematically sampled during the survey. However, it is closely related to rainforest and is likely to exhibit the same general trends in its fern flora.

Nomenclature and Taxonomy

Nomenclature and classification of species follows that given in Jones and Clemesha (1981). For convenience throughout the text, the subspecific epithets of *Asplenium trichomanes* subsp. *quadrivalens*, *Cystopteris filix-fragilis* subsp. *laetivirens* and *Grammitis magellanica* subsp. *nothofagetii* are omitted.

The taxon referred to in this work as *Asplenium* cf. *terrestre* may be either an undescribed species or conspecific with *A. terrestre* from New Zealand (P. Brownsey, comments with herbarium material, Tasmanian Herbarium). It is widespread in Tasmania and has previously been confused with *A. flaccidum* or *A. bulbiferum* (Brownsey, loc. cit.).

Grammitis pseudociliata has been included in this paper but was not found during the survey. This species, previously considered a New Zealand endemic, has only

recently been collected in Tasmania (by M. Garrett). Although only found in "mixed forest" it has been included because it is epiphytic on *Eucryphia lucida*, a common rainforest dominant.

RESULTS AND DISCUSSION

Forty nine species of pteridophytes have been recorded from Tasmanian rainforest (see Table 1). These are contained within 15 families of Pteropsida (ferns), one family of Lycopsidea (clubmosses) and one family of Psilopsida (fork-ferns). Three species, *Asplenium flabellifolium*, *Pteridium esculentum* and *Pteris tremula*, appear to be adventive and are considered doubtful rainforest species. The remaining 46 species represent just over half of the total number of pteridophytes recorded from Tasmania. The richest families in rainforest are the Blechnaceae (water ferns) and the Hymenophyllaceae (filmy ferns). Each is represented by eight species which includes all the Tasmanian species of filmy ferns and all but one of the water ferns. *Apteropteris applanata* is the only endemic fern known from Tasmanian rainforest.

Excluding adventive ferns, the rainforest pteridophytes include 27 terrestrial species (including two tree ferns) and 19 epiphytes although several species could be considered in either group, particularly some of those classified here as epiphytes. These two groups can be subdivided using some of the categories from Page's (1979) ecological classification of ferns in mesic and in xeric epiphytic environments in the tropics. Thus, three terrestrial habitats can be recognized: the forest floor, streamsides and rockfaces. Epiphytic habitats can be divided into two groups: the canopy and the understorey. The latter group comprises both crotch and main branch species (after Parris 1976) as well as those occurring below 2m. Low and high climbers, as described in Page (1979) for tropical forests, are not a feature of cool temperate rainforest in Tasmania with only one species, *Microsorium diversifolium*, occurring as a climber.

Terrestrial Ferns

Diversity among the ground ferns is usually low except in riverine situations, and in many forest communities only one or two species are present. Nevertheless, these are often abundant and may form a continuous cover up to 1m high. The most common ground ferns in undisturbed rainforest are *Blechnum watsii* and *Polystichum proliferum*. They can occur intermixed but in many forests they are mutually exclusive or almost so. They are found throughout Tasmania although the best development of *Blechnum watsii* is on the organic or infertile mineral soils of western and southwestern Tasmania whilst *Polystichum proliferum* is most characteristic of fertile mineral soils in northwestern, central and northeastern Tasmania. Both species are found across a range of altitudes, from sea level to treeless alpine situations but in extreme highland sites they are confined to sheltered positions among rocks. The tree fern, *Dicksonia antarctica*, may accompany either species although its greatest abundance and most impressive growth is seen in communities where *Polystichum* is present. *Dicksonia* is particularly common along creek and river margins, and in moist gullies or water seepages. However, its occurrence in these situations is probably related as much to soil nutrients as to moisture availability since it also occurs in drier habitats, particularly on good soils.

In upland rainforests, particularly in central and northeastern Tasmania, two smaller species, *Blechnum penna-marina* and the facultative epiphyte, *Hymenophyllum peltatum*, may be more common on the ground than either *B. watsii* or *Polystichum*. *Blechnum penna-marina* is an obligate soil-dwelling species and occurs as small scattered plants, often obscured by litter. *Hymenophyllum peltatum* forms low dense patches on mossy rocks, logs or exposed roots. A second facultative epiphyte, *Grammitis billardieri*, is often present as small scattered tufts and, like

Hymenophyllum peltatum, shows an apparent predilection for mossy surfaces. As well as these species, small patches of *Lycopodium fastigiatum* are sometimes present on the forest floor in upland forests.

Two other ground ferns, *Histiopteris incisa* and *Hypolepis rugosula*, are widespread in rainforest but are most characteristic of disturbed sites. They are able to tolerate relatively high light intensities and form a dense cover in open situations below breaks in the canopy or along roadsides and tracks. In mature well-developed rainforest they occur as occasional plants, often weak and spindly, in local spots which are better lit than the surrounding forest. *Histiopteris* is one of only a few Tasmanian ferns which "die down" during the colder winter months.

Of the remaining forest floor ferns, most are patchy or rare in rainforest. Some of the more notable species include *Diplazium australe* and *Pteris comans* which are locally common on poorly drained soils but are mostly restricted to northwestern Tasmania. *Gleichenia microphylla* also occurs in poorly drained areas, mainly where the forest is disturbed, whilst *Lindsaea trichomanoides* is sporadic on peaty soil and on logs.

The narrow fringing band of rainforest which occurs along the edges of creeks, rivers and lakes represents a separate habitat from the forest floor and often supports an abundance of ferns. Many widespread species are present, e.g. *Dicksonia antarctica*, *Polystichum proliferum* and *Blechnum watsii*, as well as several others which reach their best development in rainforest in this habitat. For example, *Blechnum vulcanicum* and *Sticherus tener* are particularly well-developed on the steep or overhanging banks of the larger streams although they are not confined to these sites. Within rainforest, *Blechnum nudum* is mostly confined to river edges, although outside of rainforest it is widespread in relatively open situations on the forest floor. *Blechnum fluviatile*, *B. minus* and *B. chambersii* are commonly associated with flowing water although occasionally they occur on rockfaces away from water. *B. chambersii* is particularly shade-loving and is rarely present where direct sunlight penetrates to the ground surface.

Rockfaces can also support a wide variety of ferns although at each individual site usually only a few species are present. The flora consists mainly of mixtures of terrestrial and epiphytic species. However, *Cystopteris filix-fragilis*, *Asplenium trichomanes* and *A. flabellifolium* appear to be restricted to this habitat and are considered characteristic of rockfaces. The most common terrestrial (including streamside) ferns are *Blechnum* spp. and these are usually represented by scattered plants on ledges or anchored in rock crevices. In open, often wet, conditions, *Blechnum vulcanicum* may form locally dense patches with many pendulous wedge-shaped fronds. *Asplenium bulbiferum* and several other less common ground ferns are also occasionally found on rockfaces. Epiphytic species present include *Asplenium* cf. *terrestre*, *Microsorium diversifolium*, *Tmesipteris billardieri*, *Lycopodium myrtifolium*, *Grammitis billardieri* and *Hymenophyllum* spp. *Hymenophyllum flabellatum* appears to be very drought tolerant and is often found on the dry roof below overhanging rocks. In high altitude situations in southwestern Tasmania the normally host-specific *Apteropteris* is sometimes abundant on rockfaces, forming a dense soft grey mat over the rock surface.

Epiphytic Ferns

Epiphytic ferns are widespread in rainforest but are usually smaller and less prominent than the ground ferns. The largest of the widespread species are *Rumohra adiantiformis*, *Asplenium* cf. *terrestre* and *Microsorium diversifolium*. Equally common but less conspicuous are members of the Hymenophyllaceae and Grammitidaceae, e.g. *Hymenophyllum rarum*, *H. peltatum* and *Grammitis billardieri*.

Very few of the ferns included in this group are obligate epiphytes and most have been found (some rarely) on rocks or soil. Exceptions include *Asplenium flaccidum*, *Polyphlebium venosum* and *Grammitis pseudociliata*.

Host specificity is poor and many vascular species can act as substrates including the forest dominants, lesser trees and some of the larger undershrubs. The thick fibrous trunks of the tree fern, *Dicksonia*, provide excellent substrates and may support all of the epiphytic ferns present at any one site. Ferns which appear to be confined to a particular host species include *Apteropteris applanata* which when epiphytic is found only on *Athrotaxis* trunks (either *A. selaginoides* or *A. cupressoides*). *Tmesipteris elongata* and *Polyphlebium venosum* have been recorded only on *Dicksonia* trunks in rainforest although the latter is also known from the trunks of *Cyathea cunninghamii* in wet sclerophyll forests. *Grammitis pseudociliata* is known in Tasmania from a single collection from *Eucryphia lucida*. *Ctenopteris heterophylla* has a wider range but when epiphytic shows a preference for *Eucryphia lucida* or *Olearia argophylla*. *Tmesipteris billardieri* is found most frequently on tree ferns but also occurs occasionally on the mossy buttresses and peaty litter cones of the larger tree species. The conifers, particularly *Phyllocladus aspleniifolius*, are poorly colonized by epiphytic ferns.

Differences in the fern flora between high and low epiphytic sites are manifest mainly in the poor development of the canopy flora. All epiphytes recorded from rainforest occur in the understorey but several appear to be very tolerant of a wide range of light and moisture conditions and extend into the canopy. However, the canopy flora is not characterized by any additional species and thus, in Tasmanian rainforest, there are no ferns which can be classed exclusively (or mainly) as high epiphytes (cf. Page 1979). Species present in the canopy are typically small ferns (*Hymenophyllum rarum*, *H. peltatum*, *H. cupressiforme*, *Grammitis magellanica*, *Ctenopteris heterophylla*) except for *Microsorium diversifolium* and occasional stunted plants of *Rumohra adiantiformis*.

Distribution

Very few ferns are restricted to rainforest in Tasmania. Exceptions include some of the uncommon species such as *Asplenium flaccidum* and *Lindsaea trichomanoides*. Many species are equally abundant in other vegetation types, particularly wet eucalypt forests and some, including *Asplenium bulbiferum*, *Lastreopsis acuminata*, *Gleichenia microphylla*, *Todea barbara* and *Cyathea australis* (possibly also *Sticherus lobatus* and *Blechnum patersonii*) are developed better outside of rainforest than within it.

Within rainforest, the distribution of ferns varies among the main rainforest groups. Callidendrous rainforest possesses the richest and most luxuriant fern flora (although this is not necessarily true at every site). It contains most of the common terrestrial and epiphytic ferns, but is especially typified by *Polystichum* and *Dicksonia* which dominate the understorey vegetation in many medium to low altitude forests. Two species are restricted to callidendrous forests, viz. the tree fern, *Cyathea australis* which, in rainforest, is confined to small relict patches mostly on the east coast, and *Tmesipteris elongata*. Several other species such as *Hymenophyllum cupressiforme* and species mainly epiphytic on tree ferns, e.g. *Hymenophyllum flabellatum*, *Polyphlebium venosum* and *Tmesipteris billardieri*, are found most commonly in callidendrous forest although they occur also in other rainforest groups.

Most fern species which are found in callidendrous forests occur also in thamnisc rainforest but they rarely attain the same luxuriance. *Blechnum wattsii*, the main ground fern, is an exception and its leathery pinnate fronds may form a dense dark green cover up to 1m high, particularly where the canopy is broken. The most common epiphytes are *Hymenophyllum rarum* and *Grammitis billardieri*. The decline in

luxuriance of the fern flora compared with that in callidendrous forests may result, in part, from the scarcity of the "popular" epiphytic substrate, *Dicksonia*. However, it may also reflect some more fundamental habitat difference, possibly one associated with humidity.

In general, ferns are poorly developed in implicate rainforest although *Blechnum watsii* is common in several communities. Many characteristic species from callidendrous and/or thamnic forests are absent or rare including *Dicksonia* (and its epiphytes), *Rumohra adiantiformis*, *Asplenium* cf. *terrestre*, *Microsorium diversifolium* and *Ctenopteris heterophylla*. However, *Grammitis billardieri*, *Hymenophyllum rarum* and *H. peltatum* are widespread and *H. australe* may be present in moister situations. *Hymenophyllum marginatum* reaches its best development in implicate rainforests although it is easily overlooked because of its small size and resemblance to some liverworts. It is absent from callidendrous forests and most thamnic forests (except riverine situations) but sometimes occurs in open montane forests.

Open montane rainforest contains an impoverished fern flora. *Grammitis poeppigiana* is restricted to this group and occurs in small patches usually in rock crevices. *Apteropteris applanata* (on *Athrotaxis* trunks) and *Hymenophyllum peltatum* (epiphytic or on mossy rockfaces) may be locally common. Other ferns are rarely present and are confined to the most sheltered, shaded microhabitats.

Although most ferns are widely dispersed throughout the state, several show restricted distributions. *Lindsaea trichomanoides* has been recorded only from southwestern Tasmania and *Grammitis pseudociliata* is even rarer, being known from only one site in southern Tasmania. *Lastreopsis hispida*, *Tmesipteris elongata*, *Pteris comans*, *Diplazium australe* and *Sticherus lobatus* are local and are found mainly in northwestern Tasmania although rare occurrences are known elsewhere. *Blechnum patersonii* is found mostly in moist gullies in northern or eastern parts of the state and *Cystopteris filix-fragilis* occurs on shaded rockfaces in central and southwestern Tasmania. A number of other species show wider distributions but are constrained by specialised habitats. For example, the distribution of *Asplenium trichomanes* is contained within areas where limestone outcrops and the distribution of *Apteropteris applanata* (in its epiphytic form) is restricted to that of its host, *Athrotaxis*. Some species, although more widely dispersed in the state, are uncommon, e.g. *Asplenium flaccidum* and *Lycopodium myrtifolium*.

As a general trend, the abundance and luxuriance of ferns declines with increasing altitude with the most pronounced effect being apparent at 600-700m above sea level. Several of the larger ground ferns, e.g. *Polystichum proliferum* and *Blechnum watsii*, may be present in rainforest above about 700m but they are represented by scattered, often small individuals which occur mostly in sheltered sites. A few species, including *Hymenophyllum peltatum*, *Grammitis billardieri*, *Blechnum penna-marina* and *Lycopodium fastigiatum*, are well-adapted to high altitude situations although not necessarily restricted to them. In montane rainforests (above 1000m), *Grammitis billardieri* is replaced by *G. poeppigiana* which occurs in small dense mats in rock crevices. *Cystopteris filix-fragilis* also appears to be restricted to upland forests (altitudes above 800m).

A similar trend of altitudinal zonation is apparent in Victorian cool temperate rainforest (see Howard & Ashton 1973) although the altitude differences occur at lower elevations in Tasmania. One species, *Hymenophyllum peltatum*, which was found only in high altitude forests in Victoria (Howard & Ashton 1973) occurs across a wide range of altitudes in Tasmanian rainforest and may be present at sea level in some riverine communities in western parts of the state.

Biogeography

The geographical distribution of ferns found in Tasmanian rainforest, taken from Jones and Clemesha (1981), is shown in Table 1. Over two thirds of the rainforest ferns are confined to Tasmania-Australia, Tasmania-New Zealand or Tasmania-Australia-New Zealand. Several additional species occurring in these regions also extend their range into the Pacific Islands. Other biogeographical elements are poorly represented but include a few Cosmopolitan, Endemic, Old World Tropics and Austral species (after Parris 1976). A comparison between Tasmania and other land masses containing cool temperate rainforest indicates that 8% of Tasmanian rainforest ferns are shared with South America, 69% are shared with New Zealand and 92% are shared with mainland Australia.

The southern affinities of the Tasmanian rainforest ferns are borne out by their occurrence within Australia. Only 11 of the 49 species (22%) are found in tropical northern Queensland whereas 57% are found in southern Queensland. Eighty six per cent occur also in New South Wales and in Victoria, the most southerly part of the Australian mainland. These figures are reduced, at least with respect to Victoria, where the comparison is restricted to the same habitat in both states. Thus, of the 40 species listed by Howard and Ashton (1973) in cool temperate rainforest in Victoria, 31 were recorded in Tasmania during the present survey. Thus, 53% of species from rainforest habitats are shared between Tasmania and Victoria. The most notable Tasmanian species absent from Victorian rainforest include *Asplenium* cf. *terrestre*, *Sticherus tener*, *Hymenophyllum marginatum* and *Grammitis magellanica*.

SUMMARY

The fern flora in Tasmania's rainforest is small and comprises 40 species (including three species which may be adventive). A few ferns are confined to rainforest but most occur also in wet eucalypt forests or scrub. The most common ferns include *Polystichum proliferum*, *Blechnum wattsii*, *Dicksonia antarctica*, *Rumohra adiantiformis*, *Microsorium diversifolium*, *Asplenium* cf. *terrestre*, *Hymenophyllum rarum* and *Grammitis billardieri* but many other species are widespread or locally common in particular situations. Some of the rarer ferns include *Lindsaea trichomanoides*, *Cystopteris filix-fragilis*, *Grammitis pseudociliata* and *Lastreopsis hispida*. Both epiphytic and ground species (including two tree ferns) are represented. In most communities, ground ferns account for the greatest biomass within the fern flora whilst epiphytes account for the greatest diversity. Only one endemic fern occurs in Tasmanian rainforest.

As a general trend, ferns decline in prominence and abundance from lowland situations to high altitudes. They also show differences in luxuriance and diversity among the four rainforest groups, with their best development in callidendrous rainforest. They are most impoverished in high altitude open montane rainforests.

Over two thirds of the ferns found in rainforest are confined to Australasia (Tasmania, Australia and New Zealand). Within Australia, the rainforest fern floras of Tasmania and Victoria are very similar with over thirty species being common to the rainforests of both states.

TABLE 1. Habitat and distribution of ferns recorded from Tasmanian rainforest. Distributions outside of Tasmania are taken from Jones and Clemesha (1981). (Abbreviations: N = New South Wales, NT = Northern Territory, NZ = New Zealand, Q = Queensland, SA = South Australia, SAF = South Africa, SAM = South America, Tas = Tasmania, V = Victoria).

Species	Habitat and Distribution
<i>Apteropteris applanata</i> A.M. Gray & R.G. Williams	On rocks or epiphytic (on <i>Athrotaxis</i>), scattered throughout western, central and southwestern Tasmania; endemic.
<i>Asplenium bulbiferum</i> Forst.f.	Mostly on soil or rocks but uncommon in rainforest; more widespread in wet sclerophyll forest, particularly in northwestern, northern, and eastern parts of the state. Q, N, V, SA, NZ, Asia.
<i>A. flabellifolium</i> Cav.	Uncommon in rainforest and probably adventive; mostly found among rocks in drier forests. All states, NZ.
<i>A. flaccidum</i> Forst.f.	Epiphytic, scattered in rainforest throughout Tas. Q, N, V, NZ, Pacific Is.
<i>A. trichomanes</i> L. subsp. <i>quadrivalens</i> D.E. Meyer	Restricted to limestone rocks; present in several vegetation formations. All states except Q, NZ, Europe.
<i>A. cf. terrestre</i>	A widespread epiphyte in rainforest.
<i>Blechnum chambersii</i> Tindale	Ground species of shady situations in wet forests mostly along rivers or drainage channels but also on rockfaces. Q, N, SA, NZ, Fiji.
<i>B. fluviatile</i> (R.Br.) E.J. Lowe ex Salom.	Widespread ground species in wet forests near creeks but also on rockfaces. N, V, NZ.
<i>B. minus</i> (R.Br.) Ettingsh.	Common ground species along creeks. Q, N, V, SA, NZ.
<i>B. nudum</i> (Labill.) Mett. ex Luerss.	Widespread ground species; in rainforest, mostly along edges of creeks and rivers where the canopy is broken. Q, N, V, SA.
<i>B. patersonii</i> (R.Br.) Mett.	Ground species; local, near creeks in wet forests in northern and eastern Tasmania. Q, N, V, Fiji.
<i>B. penna-marina</i> (Poir.) Kuhn	Widespread ground species in high altitude situations in several vegetation formations; occasionally found to sea level. N, V, NZ, SAM, SubAntarctic Is.
<i>B. vulcanicum</i> (Bl.) Kuhn	Ground species, most common along the edges of creeks and rivers in western and southwestern Tasmania; also on rockfaces. NZ.
<i>B. wattsii</i> Tindale	Widespread ground species in wet forests. Q, N, V, SA.
<i>Ctenopteris heterophylla</i> (Labill.) Tindale	Epiphytic or on rocks; scattered in wet forests but also extending into drier vegetation. V, NZ.
<i>Cyathea australis</i> (R.Br.) Domin	Tree fern; occasional in rainforest but common in wet eucalypt gullies in eastern, northeastern and northern Tasmania. Q, N, V.
<i>Cystopteris filix-fragilis</i> (L.) Bernh. subsp. <i>laetivirens</i> (Prent.) C.Chr.	Occasional on rocks in central and southwestern Tasmania in high altitude forests. N, V, NZ.
<i>Dicksonia antarctica</i> Labill.	Tree fern; widespread in wet forests. Q, N, V, SA.
<i>Diplazium australe</i> (R.Br.) N.A. Wakefield	Ground fern; patchy in wet forests, mainly in northwestern Tasmania. Q, N, V, NZ.
<i>Gleichenia microphylla</i> R.Br.	Ground fern; occasional in rainforest, widespread in damp situations in other wet forests. All states, NZ.
<i>Grammitis billardieri</i> Willd.	Epiphytic or terrestrial; widespread in wet forests. N, V, NZ, SAF, SAM.
<i>G. magellanica</i> Desv. subsp. <i>nothofagetii</i> Parris	Scattered in wet forests, mainly epiphytic. NZ.

<i>G. poeppigiana</i> (Mett.) Pic. Ser.	Scattered in high altitude vegetation, usually in sheltered rock crevices. N, V, NZ, SubAntarct. Is.
<i>G. pseudociliata</i> Parris	Epiphyte known from one location only in Tasmania. NZ.
<i>Histiopteris incisa</i> (Thunb.) J.Sm.	Ground fern; widespread in wet forests. Q, N, V, SA, NT, Tropics & S. Hemisphere.
<i>Hymenophyllum australe</i> Willd.	Common in wet forests, mostly on buttresses or mossy rocks where the humidity is high. Q, N, V.
<i>H. cupressiforme</i> Labill.	Usually epiphytic; widespread in wet forests. Q, N, V.
<i>H. flabellatum</i> Labill.	Mostly an epiphyte of <i>Dicksonia</i> , but also on logs or rocks. Q, N, V, NZ, Pacific Is.
<i>H. marginatum</i> Hook. & Grev.	Mostly epiphytic in western and southwestern Tasmania, in wet scrub and forests. Q, N.
<i>H. peltatum</i> (Poir.) Desv.	Widespread epiphytic or rock species in wet forests; common at high altitudes but also extending to sea level. Q, N, V, NZ, SAf, Mascarene Is. (Also in S. Chile — Looser 1948).
<i>H. rarum</i> R.Br.	Widespread in wet forests; mainly epiphytic. N, V, NZ.
<i>Hypolepis rugosula</i> (Labill.) J.Sm.	Widespread ground fern in wet forests. Q, N, V, SA, NZ.
<i>Lastreopsis acuminata</i> (Houlston) Morton	Ground fern; uncommon in rainforest but more widespread in other wet forests. Q, N, V, SA.
<i>L. hispida</i> (Sw.) Tindale	Ground fern; sporadic, mostly in northwestern Tasmania along creeks. N, V, NZ.
<i>Lindsaea trichomanoides</i> Dryand.	Localized in rainforests in southern and southwestern Tasmania, mostly along the larger rivers. N, V, NZ.
<i>Lycopodium fastigiatum</i> R.Br.	Widespread ground species in upland vegetation. Q, N, V, NZ.
<i>L. myrtifolium</i> Forst.f.	Occasional in wet forests; epiphytic or terrestrial. Q, N, V, NZ.
<i>Microsorium diversifolium</i> (Willd.) Copel.	Widespread across a range of vegetation types including dry forests; epiphytic or terrestrial. Q, N, V, NZ, Norfolk Is.
<i>Polyphlebium venosum</i> (R.Br.) Copel.	Epiphyte; restricted to <i>Dicksonia antarctica</i> trunks in rainforest but also on <i>Cyathea cunninghamii</i> trunks in wet eucalypt forests. Q, N, V, NZ.
<i>Polystichum proliferum</i> (R.Br.) Presl	Widespread ground fern in wet forests. N, V, SA.
<i>Pteridium esculentum</i> (Forst.f.) Cockayne	Ground fern; adventive in rainforest, common in other wet and dry lowland vegetation. All states, NZ, Pacific Is.
<i>Pteris comans</i> Forst.f.	Ground fern; patchy in rainforest, mainly found in northwestern Tasmania. Q, N, V, NZ, Pacific Is.
<i>P. tremula</i> R.Br.	Uncommon ground fern in Tasmania, probably adventive in rainforest. Q, N, V, SA, NT, NZ, Norfolk Is, Fiji.
<i>Rumohra adiantiformis</i> (Forst.f.) Ching	Widespread terrestrial and epiphytic species. Q, N, V, NZ, SA, SAf
<i>Sticherus lobatus</i> N.A. Wakefield	Ground fern; patchy in rainforest, mostly in forests from north-western Tasmania. Q, N, V.
<i>S. tener</i> (R.Br.) Ching	Widespread ground fern in wet forests, often found along rivers or road cuttings. N, V.
<i>Tmesipteris billardieri</i> Endl.	Widespread in wet forests, usually epiphytic on <i>Dicksonia antarctica</i> but occasionally in peat or on logs. N, V.
<i>T. elongata</i> Dang.	Recorded only from <i>Dicksonia</i> trunks; occasional in lowland Tasmania but possibly overlooked. V, NZ.
<i>Todea barbara</i> (L.) T. Moore	Ground fern; uncommon in rainforest, found elsewhere along creeks and in gullies mostly in drier lowland parts of the state. Q, N, V, SA, NZ, SAf.

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TMESIPTERIS IN VANUATU (NEW HEBRIDES)

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ABSTRACT

Cytological, anatomical and ecological observations on *Tmesipteris* from Vanuatu are presented and attention is drawn to the variation in stem anatomy and ecology in the genus as a whole. Three species are recognised in the archipelago: *T. oblongifolia* sp. nov. (n = 104) from Tanna and Aneityum, *T. vanuatensis* sp. nov. (n = 104) from Espiritu Santo and *T. oblanceolata* (R.Br.) Desv. (n = 208) from Aneityum and Espiritu Santo.

INTRODUCTION

The genus *Tmesipteris* was based by Bernhardt (1801) on the species, *Lycopodium tannense*, which was described a year earlier by Sprengel (1800) from a Forster collection supposedly made on Tanna, Vanuatu. However, no Forster specimen from Tanna has ever been found and Sprengel's description is very brief and only sufficient to place the species in the genus. *Tmesipteris* was collected again in the archipelago by both Milne and Seeman in the middle of the last century but these collections came from Aneityum and differed from Bernhardt's description and illustration. Consequently the identity of the type species, *T. tannensis* (Spreng.) Bernh., remained for many years in doubt and our knowledge of the genus in the islands as a whole has been based on very few specimens and was inevitably incomplete.

Recently *Tmesipteris* has been found again on Tanna, Aneityum and, for the first time, on Espiritu Santo. The new material from Tanna has already clarified the typification and identity of *T. tannensis*. It differs from the species illustrated by Bernhardt (1801) and Chinnock (1976) has provided convincing evidence to show that the Forster specimen described and illustrated by Bernhardt in fact came from Dusky Sound, New Zealand, and has suggested that the reference to Tanna by Sprengel was probably an error. The Bernhardt illustration is, therefore, selected as the neotype of *L. tannense* Spreng. and the type species is now considered to be restricted to New Zealand.

The present paper gives a more complete account, including cytological and anatomical studies, of *Tmesipteris* in Vanuatu. The material from Tanna belongs to the *T. lanceolata* group and is described as a new species, *T. oblongifolia*, which is also found on Aneityum. Two further species are also recognised in the archipelago, namely, *T. vanuatensis* A.Braith. a new species proposed for material from Espiritu Santo, and *T. oblanceolata* (R.Br.) Desv. from Aneityum and Espiritu Santo.

MATERIALS AND METHODS

The material was collected by the author during the 1971 Royal Society and Percy Sladen Expedition to the New Hebrides. The details of the localities of the collections are given in Table 1. At each locality plants were collected for herbarium specimens and preserved in 70% alcohol for anatomical studies. When available, sporangial material was also fixed in the field in 1:3 acetic-alcohol and despatched by air to the U.K. where it was stored in a deep freeze. Meiotic preparations for chromosome counts were subsequently made using the acetocarmine squash method. The material for anatomical studies was embedded in paraffin wax and the sections stained in safranin and light green or aniline blue. Spore samples were taken from dried herbarium specimens and mounted in gum chloral for measurement. Herbarium material of each species is deposited in the Herbarium, Royal Botanic Gardens, Kew.

CYTOLOGY

The results of the chromosome counts are summarised in Table 1 and representative cells are illustrated in Figs. 1 & 2. It is difficult to produce absolutely unequivocal counts in the genus because of a) the high chromosome numbers, b) variation in the size of chromosomes and c) the sometimes peculiar shapes of the bivalents. The latter has generally been attributed to a laxity in the spiral structure (Manton 1950, Lovis 1977). Nevertheless the counts listed in Table 1 are accurate to within one or two chromosomes except where indicated, and even in these cases the order of the chromosome number is not in doubt.

TABLE 1. Chromosome Numbers in *Tmesipteris* from Vanuatu

Species	Locality	Chromosome number	Spore length* (µm)	Length of Stomata* (µm)
<i>T. oblongifolia</i>	RSNH 2146, Woptiabo, Aneityum	n = 104	62.7 ± 4.2	96.0
	RSNH 2204, Mt. Toukosmeru, Tanna	n = 104	57.5 ± 3.3	92.5
	RSNH 2211, Mt. Toukosmeru, Tanna	n = 104	57.4 ± 3.8	—
<i>T. vanuatuensis</i>	RSNH 2354, Apouna Valley, Espiritu Santo	n = 104	62.0 ± 3.6	93.2
	RSNH 2382, Mt. Tabwemasana, Espiritu Santo	n = c.104	58.6 ± 3.6	92.3
<i>T. oblanceolata</i>	RSNH 2112, Inrero, Aneityum	n = 208	82.8 ± 4.1	133.4
	RSNH 2152, Nezwon Nelgon, Aneityum	n = c.208	81.5 ± 4.3	123.6

* Data based on 100 measurements from one specimen from each collection.

The numbers recorded here fall into the cytological pattern already established for the genus by Barber (1957) from Australian material of two groups with $n = 104$ and $n = 208$ respectively. These relatively high numbers have in the past been designated as various levels of polyploidy but are here interpreted in terms of the lowest extant number known in the Psilotales, which is $n = 52$ (Lovis 1977). Thus *T. oblongifolia* and *T. vanuatuensis* are tetraploids and *T. oblanceolata* is an octoploid.

The mean length of spores and stomata are also given in Table 1. It is clear from this data that the spores and stomata of the octoploid, *T. oblanceolata*, are considerably larger than those of the tetraploids, *T. oblongifolia* and *T. vanuatuensis*. Although the samples are small, the data do suggest that these microcharacters are potentially useful in Vanuatu as polyploid indicators.

ANATOMY

The species from Vanuatu show the basic vascular pattern described from other *Tmesipteris* species (Sykes 1908, Sahni 1925). Thus the solid core of tracheids in the rhizome becomes medullated and breaks up in the transition region to form a variable number of groups of tracheids arranged around a central pith. The representative sections illustrated in Fig. 3 show the typical arrangement of the stele at the top of the transition region. In all three species groups of tracheids can be seen surrounding a well defined pith. There are, however, differences in the nature of the pith cells and two basic types can be recognised.

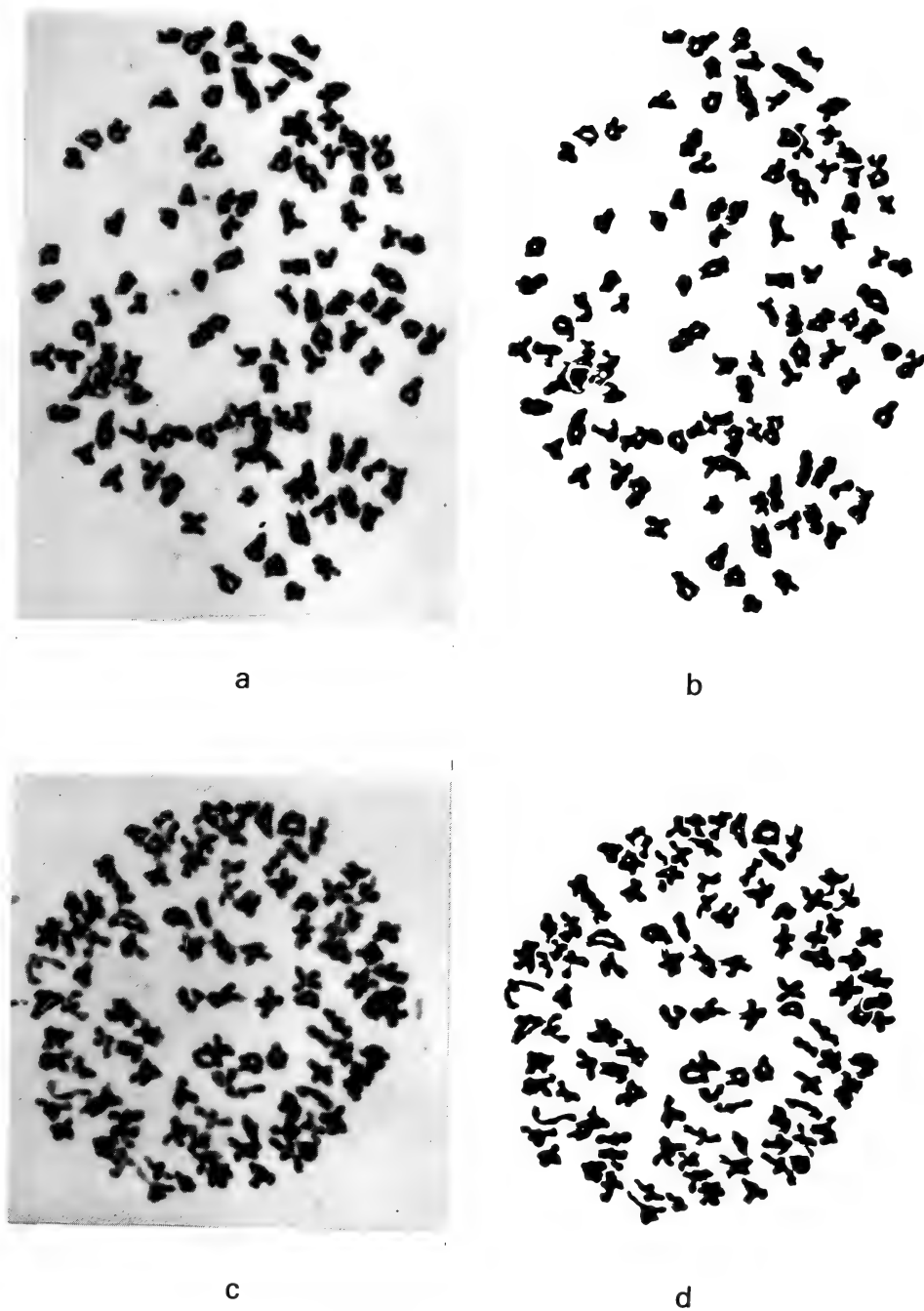


FIGURE 1. Permanent acetocarmine preparations for meiosis. X 750. a) *T. oblongifolia* RSNH 2204. b) Explanatory diagram showing 104 bivalents. c) *T. vanuatuensis* RSNH 2354. d) Explanatory diagram showing 104 bivalents.

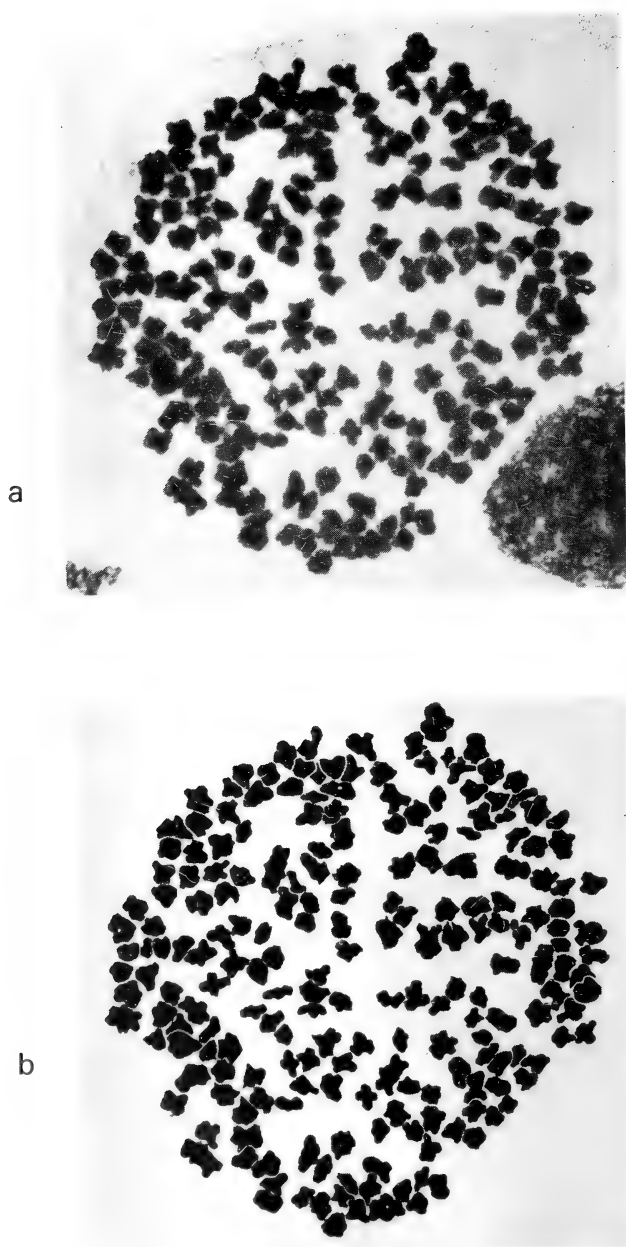


FIGURE 2. Permanent acetocarmine preparation of meiosis. X 750. a) *T. oblaneolata* RSNH 2112. b) Explanatory diagram showing 208 bivalents.

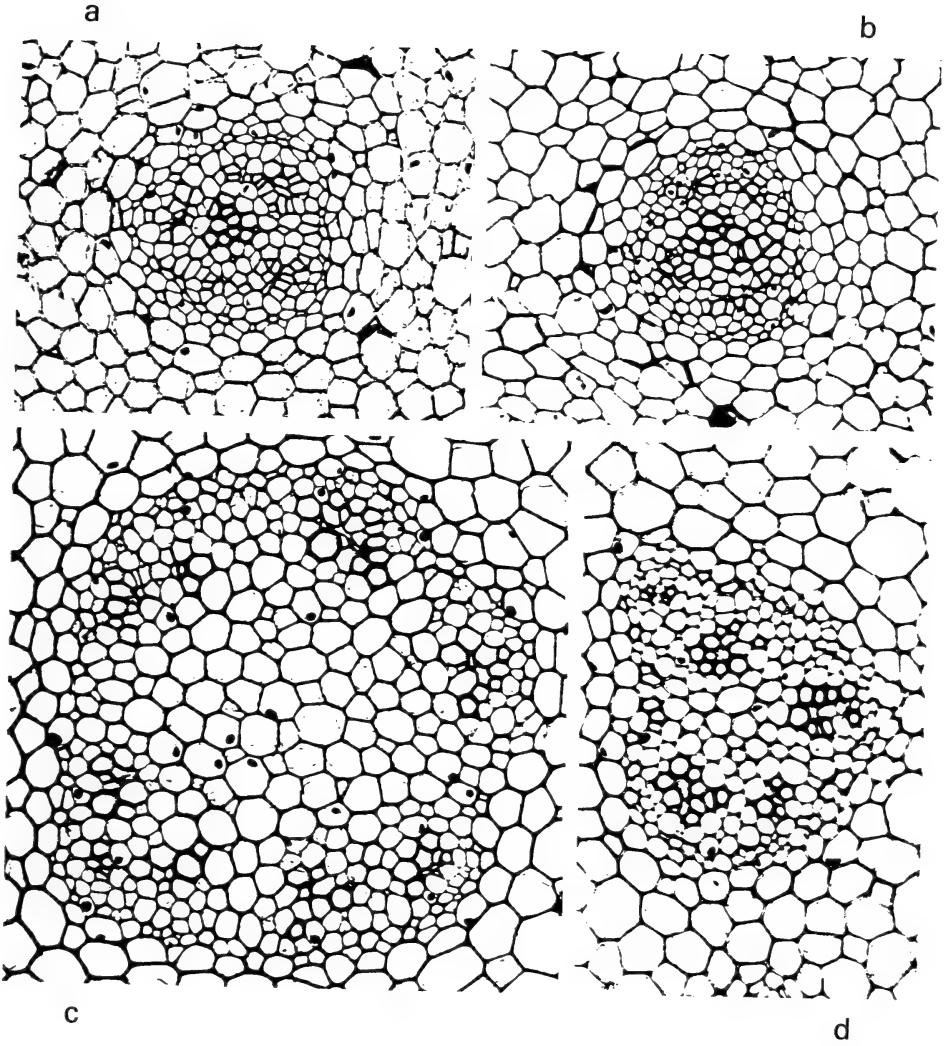


FIGURE 3. Transverse sections of aerial shoots of *Tmesipteris* species from Vanuatu. X 100. a) *T. oblongifolia* RSNH 2204. b) *T. vanuatuensis* RSNH 2382. c) & d) *T. oblanceolata* RSNH 2112. a, b & c from top of transition region; d from distal part of aerial shoot.

The first type is illustrated by *T. oblongifolia* (Fig. 3a) and *T. vanuatensis* (Fig. 3b). In these species the pith is small and made up of narrow thick walled, lignified cells which in transverse sections have the same appearance as fibres or sclerenchyma. The tracheids around the pith are by contrast thinner walled and the tracheid bundles can be located in the sections by their mesarch protoxylem. The second type of pith is characteristic of *T. oblanceolata* (Fig. 3c,d). Here the groups of tracheids surround a relatively large pith made up of thin walled parenchymatous or slightly collenchymatous cells. Even in the distal parts of the leafy shoot, where the number of tracheid bundles and pith are much reduced, the pith cells are still essentially parenchymatous (Fig. 3d). Medullary xylem has been found associated with this type of pith in *T. vieillardii* (Sahni 1925) from New Caledonia and *T. oblanceolata* (Braithwaite 1973) from the Solomon Islands, but none has been found in the material from Vanuatu. On present evidence the pith type appears to be constant for each species.

Variations in the pith cells in the stems of other *Tmesipteris* species have been reported by a number of previous investigators, notably Dangeard (1890-91), Sahni (1925) and Braithwaite (1973). In all cases two types of pith composed of either parenchymatous cells or sclerenchymatous cells have been recognised. The consistency of the observations so far suggests that this recently rather neglected anatomical character perhaps merits further investigation to establish whether it may be useful as a taxonomic indicator, either at the species level or for the grouping of species.

ECOLOGY AND DISTRIBUTION

During the 1971 Royal Society and Percy Sladen Expedition to the New Hebrides *Tmesipteris* was encountered only sporadically in montane forest at altitudes of 475-745m on Aneityum and Tanna in the south and 900-1650m on Espiritu Santo in the north. However, many of the other larger islands in the group attain altitudes in excess of 500m so that it can perhaps be anticipated that further collecting will extend its distribution within the islands.

T. oblongifolia and *T. vanuatensis* were confined almost exclusively to the lower parts of the tree fern trunks belonging to the genus *Cyathea*. Both species were recorded from *C. lunulata*, but they were also collected from other *Cyathea* species so that they do not appear to be confined to any particular species.

Unlike the other two species, *T. oblanceolata* was never found on tree ferns. It grew among mosses and filmy ferns on the trunks of angiospermous trees such as *Metrosideros* and *Weinmannia* (see Fig. 1b in Braithwaite 1975) or out of organic accumulations beneath epiphytic ferns such as *Asplenium nidus*. *T. oblanceolata* has also been recorded on decayed wood on the forest floor (Milne 272K). Non-tree-fern substrates have been reported for *Tmesipteris* species elsewhere; notably *T. vieillardii* of New Caledonia (Sahni 1925), *T. tannensis* (Spreng.) Bernh. s. strict. in New Zealand (Chinnock 1976) and *T. oblanceolata* from the Solomon Islands (Braithwaite 1973).

It is becoming increasingly clear that speciation within the genus has been accompanied by some ecological differentiation, although the extent to which the latter may be useful in delimiting species or determining species relationships is at present not clear.

KEY TO THE SPECIES

Aerial shoots 6-16cm long, leaves ovate-oblong or narrowly oblong to elliptic.

Leaves ovate-oblong with obtuse apices,
l/b ratio < 3, distichously arranged
beyond the sporophylls.

T. oblongifolia

Leaves narrowly oblong to elliptic with
acute apices, l/b ratio > 3, spirally
arranged beyond the sporophylls.

T. vanuatensis

Aerial shoots 15-38cm, leaves narrowly
rectangular to narrowly obovate with
truncate or rounded apices.

T. oblanceolata

***Tmesipteris oblongifolia* A. Braith. sp. nov.**

Planta epiphytica in truncis filicum arborum. Surculus aeris simplex, pendulus, (6-)8-14(-16)cm longus, per unum crescentem maturescens, folio magno terminati. Folia infra sporophylla spiraliter disposita, supra sporophylla disticha disposita, subcoriacea, (7-)9-13(-15)mm longa, (3-)3.5-4.5(-5)mm lata, ovato-oblonga, apicibus rotundatis obtusis mucronatis. Sporophylla spiraliter disposita, medianum caulis foliosi occupantes, longitudine folia aequantia. Synangium 2-4mm longum, sporangiis lobiis aequalibus. Sporae bilaterales, monoletae, concavo-convexae, (51-)57-62(-73) μ m longae, (18-)21-22(-25) μ m latae. Chromosomatum numerus gametophyticae 104.

Holotype: Tanna, W ridge of Mt. Toukosmeru (19°33'S 169°21'E), 500m, epiphyte on *Cyathea* trunk (same sp. as RSNH 2184), 28 Jul. 1971, A.F. Braithwaite RSNH 2204 (K).

Plant epiphytic on trunks of tree ferns. Aerial shoots simple, pendulous, (6-)8-14(-16)cm long, maturing in one growing season and terminating in large leaf-like appendage. Leaves spirally arranged below the sporophylls, distichously arranged in portion of leafy shoot distal to the sporophylls, 3-4 per cm stem, subcoriaceous, (7-)9-13(-15)mm long, (3-)3.5-4.5(-5)mm wide, ovate-oblong with rounded obtuse mucronate apex. Sporophylls spirally arranged, 5 per cm stem, occupying the middle of the leafy part of the shoot or throughout the upper two thirds, \pm equal in length or slightly shorter than the leaves. Synangia 2-4mm long, 1-1.5mm high, with lobes of sporangia approximately equal, \pm globular. Spores bilateral, monolete, concavo-convex, (51-)57-62(-73) μ m long, (18-)21-22(-25) μ m broad. Chromosome number $n = 104$.

T. oblongifolia is closely allied to *T. lanceolata* from New Caledonia and New Zealand. The two species are similar in size and share a distichous arrangement of leaves in that portion of the leafy shoot distal to the sporophylls. The two species also possess the same pith type in the stem and chromosome number. Dangeard (1890-91) describes and illustrates the pith cells of *T. lanceolata* as "fibres medullaires" and unpublished chromosome counts by the author show it to be a tetraploid. *T. oblongifolia* can however be distinguished by its thinner texture, ovate-oblong leaves with an obtuse apex and by the position of the sporophylls, which are found in the middle or upper two thirds of the leafy shoot and never only at the base or in the lower half as in *T. lanceolata*.

Distribution: Philippines, Vanuatu and the Marquesas.

Specimens examined:

VANUATU. Aneityum, ridge leading to Woptiabo, c.5km ENE of Anelcauhut (20°13'S 169°49'E), 487m, epiphytic on *Cyathea lunulata* in ridge side forest, 23 Jul. 1971, Braithwaite RSNH 2146 (K). Tanna, W ridge of Mt. Toukosmeru (19°33'S 169°21'E), 644m, epiphytic on base of large *Cyathea lunulata*, 28 Jul. 1971, Braithwaite RSNH 2211 (K).

MARQUESAS. Feani, vieux sentier 'Atuona à Hanamenu, haute vallée côte Hanamenu, 850m, brousse fougères arborescentes et *Freycinetia*, épiphyte sur les bases de fougères arborescentes, assay rare, 5 Mar. 1975, Schafer & Oline 5272 (K);

Chemin d'Omoa à Hanavave, crête principale, mont Moratina (Mt. Boïse de la carte), 670m, brousse assy humide avec *Cyathea*, *Crossostylis*, sur bases de *Cyathea*, assy rare, 18 Sept. 1975, Schafer 5758 (K); Feani, montagnes entre la haute vallée de Hanamenu et la crête de Temetiu, 900m, petit haut vallée à forêt très humide: *Crossostylis*, *Cyathea*, *Pandanaceae*, *Weinmannia*, *Myrsine*, sur troncs de *Cyathea*, assy rare, 23 Oct. 1975, Schafer 5914 (K); Nukuhiva, Quayle 1305 (K). PHILIPPINES. Mindanao, Davao Dist: Mt. Apo 6000ft, epiphyte always on trunks of tree ferns, Oct. 1904, Copeland 1433 (K); Mt. Apo, May 1909, Elmer 10600 (BM, K); Mt. Apo, 9000ft, Feb. 1929, Hachisaka s.n. (BM); Mt. Apo, 1800m, 1932, Copeland 203 (BM).

***Tmesipteris vanuatensis* A. Braith. sp. nov.**

Planta epiphytica in truncis filicum arborum. Surculis aerius simplex, pendulus, (6-)8-15(-16)cm longus, foliis et sporophyllis spiraliter dispositis et folio magno terminatis. Folia subcoriacea, 8-14mm longa, 2.5-3.5mm lata, anguste oblonga vel anguste elliptica, apicibus acutis et mucrone setaceo 0.5-1.0mm longo. Sporophylla medianum caulis foliosi occupantes, longitudine folia subaequantia. Syngangium parvum, 3-3.5mm longum, globosum, sporangiis lobis aequantibus. Sporae monoletae, concavo-convexae, (50-)59-62(-67) μ m longae, (18-)21(-25) μ m latae. Chromosomatum numerus gametophyticae 104.

Holotype. Espiritu Santo, crest of NW ridge of Mt. Tabwemasana, c. 1600m, epiphyte on *Cyathea* sp. in ridge top *Metrosideros*-*Weinmannia* forest, 2 Sept. 1971, A.F. Braithwaite RSNH 2382 (K).

Plant epiphytic on the trunks of tree ferns. Aerial shoots simple, pendulous, (6-)8-15(-16)cm long, maturing in one growing season, with leaves and sporophylls spirally arranged and terminating in a large leaf-like appendage. Leaves subcoriaceous, 8-14mm long, 2.5-3.5mm, narrowly oblong or ovate-oblong to narrowly elliptical with acute apices and bristle-like mucro 0.5-1.0mm long. Sporophylls occupying the middle or throughout leafy part of shoot, equal to or slightly shorter than the leaves. Syngangia 3-3.5mm long, globose, persistent, with two equal sporangial lobes. Spores monoletate, concavo-convex, (50-)59-62(-67) μ m long, (18-)21(-25) μ m broad. Chromosome number $n = 104$.

T. vanuatensis can be distinguished from *T. oblongifolia* by its spirally arranged narrowly oblong to almost elliptical leaves with a larger length/breadth ratio and generally acute apices. The leaves are also more widely spaced and arise from the stem at a more acute angle giving the plant a generally more lax and slender appearance than *T. oblongifolia* (Fig. 4).

Known only from Mt. Tabwemasana, Espiritu Santo.

Other specimen examined:

Espiritu Santo. Camp site no. 4, Nokovula Village, 23k SSW of Malau, Big Bay (15°20'S 166°44'E), disturbed forest area below village, c. 900m, epiphyte on *Cyathea lunulata*, 1 Sept. 1971, Braithwaite RSNH 2354 (K).

Tmesipteris oblanceolata Copel., Philip. J. Sci. 60: 99 (1936); A. Braith., Brit. Fern Gaz. 10: 296 (1973).

Type: Solomon Islands, Guadalcanal, Tutuve Mt, 1700m, Kajewski 2632 (A).

Plants epiphytic on angiospermous tree trunks or growing on moss covered decaying wood on forest floor. Aerial shoots simple, pendulous or occasionally sub-erect, (15-)20-30(-38)cm long, maturing in a single growing season and terminated by a small leaf-like appendage; transition region (4-)5-10(-11)cm long; leaves and sporophylls spirally arranged and often tending to decrease in size towards the apex. Leaves (10-)11-14(-16)mm long, 2.5-3.5mm broad, coriaceous to subcoriaceous, (4-)5(-6) per cm stem, narrowly oblong or rectangular but narrowing towards the base to narrowly obovate, \pm falcate, apex truncate and sometimes bilobed to rounded, mucronate; mucro stiff, 1-2mm long. Sporophylls developed in mid region or throughout upper two thirds of leafy shoot, equal in length to leaves; syngangia 3-4mm long, 1.5-2mm high, persistent, bilocular, sporangial lobes \pm equal. Spores monoletate, concavo-convex, (73-)81-83(-94) μ m long, (25-)31(-36) μ m broad. Chromosome number $n = 208$.

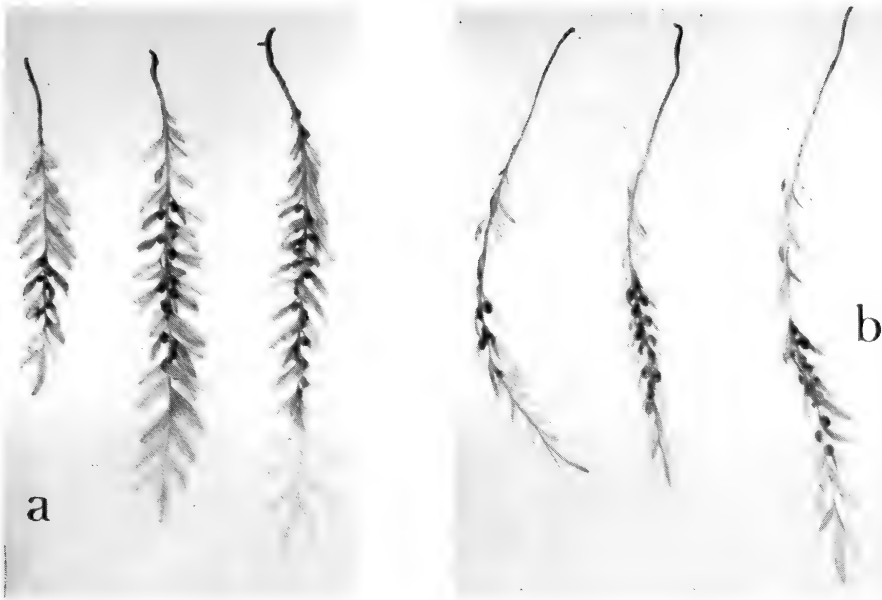


FIGURE 4. a) *T. oblongifolia* RSNH 2204. b) *T. vanuatensis* RSNH 2382. Specimens preserved in alcohol. X 1/2.

T. oblongifolia in Vanuatu is rather variable with respect to length of the aerial shoot and in size and shape of the leaves. The plants from Espiritu Santo with aerial shoots up to 26cm long bearing short narrowly obovate leaves with rounded apices, are virtually indistinguishable from *T. oblongifolia* Copel. from the Solomon Islands, except that medullary xylem found in specimens from the Solomon Islands (Braithwaite 1973) was not found in the single specimen available for sectioning from Espiritu Santo. The pith is otherwise of a similar parenchymatous type. The more extensive collections from Aneityum have aerial shoots up to 38cm long, some possessing narrow slightly obovate leaves with rounded apices, while the majority have longer, narrowly rectangular leaves with truncate apices. Similar variation is evident in material attributed here to *T. oblongifolia* from New Caledonia and Samoa.

The plants from Aneityum, with leaves with markedly truncate sometimes almost bilobed apices, are very similar to the Australian species *T. truncata* (R.Br.) Desv. They also share the same chromosome number. Barber (1957) reported a chromosome number of $n = 201-211$ for *T. truncata* from several different localities in New South Wales and $n = 208$ has been found here in material from Aneityum. There are however some ecological and anatomical differences. The plants from Aneityum are either epiphytic on angiospermous trees or terrestrial on decayed wood while *T. truncata* from Australia is generally, though not exclusively, epiphytic on tree ferns. There are two specimens from Australia at Kew collected from non-tree-fern substrates; one with typical truncate leaves labelled "Macquarie Harbour, humid rocky banks B mountains in shaded woods, 1825, Cunningham 92"; and the other with more oblongifoliate leaves labelled "Head of Clyde River, 25 miles SSW of Howra, 2000ft, on mossy ledge of sandstone cliff, 2 May 1937, Rodway 2369". The anatomical difference concerns the pith type in the stem. Dangeard (1890-91) reported a sclerenchymatous

pith type in *T. truncata* from Australia which differs from the parenchymatous pith found here in the material from Vanuatu. However Dangeard (in contrast to the often very detailed drawings from the stems of the other species he examined) shows only a very small outline tissue sketch for the stem of *T. truncata* (Plate XIV, Fig. 11) and it would be desirable to have the detail confirmed for material both from tree-fern trunks and from non-tree-fern substrates. It is possible that variation in the pith type may be correlated with differences in ecology.

T. oblancoolata and *T. truncata* are clearly very closely related and they probably represent forms of the same species. However on present evidence it is difficult to assess the extent or taxonomic significance of their ecological and anatomical differences. Future studies may well confirm their conspecificity but it is considered preferable for the time being to segregate the Pacific material under *T. oblancoolata*.

Distribution: New Caledonia, Vanuatu, Solomon Islands, Fiji, Samoa.

Specimens examined:

VANUATU. Aneityum: ridge crest N of Woptiabo, S end of Nithuon Nelvau (20°13'S 169°49'E), 640m, ridge top forest with *Metrosideros*, epiphytic on large leaning tree on ridge top growing underneath a large plant of *Asplenium nidus*, 23 Jul. 1971, Braithwaite RSNH 2152 (K); c. 5km NE by N of Anelcauhaut, on crest of ridge running S from Inrero (20°11'S 169°47'E), 745m, epiphytic on trunk of *Metrosideros*, occasionally on forest floor, 21 Jul. 1971, Braithwaite RSNH 2112 (K); high grounds, decayed trees, Nov. 1853, Milne 272 (K); 1854, Seeman s.n. (BM); crête S de l'Inrero, alt. 750m, epiphyte au bas de troncs, fronde portée ± horizontalement, 23 Jul. 1971, Raynal RSNH 16147 (K). Espiritu Santo: northern ridge of Mt. Tabwemasana (15°22'S 166°45'E), 1650m, low forest on ridge crest, *Weinmannia* dominant, 4 Sept. 1971 Raynal RSNH 16386 (P).

SOLOMON ISLANDS. Guadalcanal, Mt. Popomanaseu, halfway between upper camp and Vunuvelakama, c. 5000ft, growing erect in moss around base of trees in ridge top moss forest, 3 Nov. 1965, Braithwaite RSS 4782 (K).

NEW CALEDONIA. Mt. Koghi, kauri ft. 1000ft, on prostrate decaying trunk covered with liverworts, 13 Jun. 1914, Compton 764 (BM).

LORD HOWE ISLAND. Epiphyte on the top of Mt. Gower in mist forest, 2600ft, Aug. 1965, Game 65/1/SN (K).

SAMOA. May 1876, Whitmee s.n. (K).

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EFFECTS OF SALINITY ON GAMETOPHYTE GROWTH OF *ACROSTICHUM AUREUM* AND *A. DANAEIFOLIUM*

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ABSTRACT

Spore germination and gametophyte growth under salinity regimes varying from 0.0 to 3.0% NaCl was studied to determine the stress tolerance of the gametophyte generation. Responses of both New World species of *Acrostichum* are similar to those of other mangrove species which have been studied. *A. aureum* has slightly greater tolerance to increased salinity than *A. danaeifolium*. Growth responses of *A. aureum* suggest it can be classified as a true halophyte, whereas those of *A. danaeifolium* suggest it is a semi-halophyte. The response of the gametophyte generation of these species to salinity parallels the natural habitats of the sporophyte generation.

INTRODUCTION

Halophytes are notably rare in pteridophytes. The most well known example is the mangrove fern genus *Acrostichum*. There are three species circumscribed in this genus, each with different apparent tolerance to salinity. The observed habitat variation of the species forms a continuum from fresh water to inundation by tides and sea water. The most widely distributed species is *A. aureum* L., circumtropical in distribution and frequently forming large colonies in mangrove swamps, salt- and brackish-marshes, and low hammocks near sea water (Holttum 1955; Small 1938; Walsh 1974). The remaining two species are much more restricted in distribution. In tropical Asia and Australia, *A. speciosum* Willd. occurs in mangroves (Walsh 1974) frequently inundated by tides and has a greater tolerance for sea water than *A. aureum* (Holttum 1955). *Acrostichum danaeifolium* Langsd. & Fisch. is distributed in the New World tropics and subtropics in fresh or brackish water swamps, lakes, and ditches and along canal margins (Adams and Tomlinson 1979). This species is frequently found inland from coastal regions, sometimes associated with pines and palms or other glycophytes.

One of the primary factors determining the growth and distribution of plants in salt marsh habitats is the level of soil salinity (Jefferies *et al.* 1979). Other factors include both intraspecific and interspecific competition, especially when species may be only facultative halophytes. Barbour (1970) has questioned whether all halophytes are just facultative halophytes and has suggested that the ability to reproduce under "halophytic" conditions should be the ultimate criterion of salt tolerance. In halophytic pteridophytes, for sexual reproduction to be successful the gametophytic and sporophytic generation must succeed. Therefore, both generations should exhibit parallel tolerances to stress under soil salinity, assuming that the soil salinity conditions of the gametophytic and sporophytic habitats parallel one another. However, Ungar (1978) has reported that surface soils may have salinities from two to 100 times that of subsoils. Thus, the gametophytic stage may be critical if a species is to successfully inhabit a saline environment.

In the New World, collections have been made of both *Acrostichum* species. Gametophytes originating from spores of these plants as well as from the fresh water aquatic, *Ceratopteris thalictroides* (L.) Tod., have been grown under a variety of salinity conditions to test the hypothesis that tolerance to salinity by the gametophytic generation will parallel the habitat conditions in which the sporophytes occur.

MATERIALS AND METHODS

Spores utilized in this study were collected from the following locations: *A. aureum*: culture 190, Jamaica, Westmoreland Parish, 0.25 mile east of Negril on road to Savana la Mar. Plants occur densely in a large population in a lowland coastal swamp which is periodically inundated by tides; culture 193, Panama (Canal Zone), very large population of over 3000 individuals in mangrove swamp about 0.2 mile from road to Colon on road to Coco Solo; culture 150, Florida, Dade Co., 30.5 miles southwest of entrance of Everglades National Park, at road to Westlake, growing in Rhizophora-swamp; *A. danaeifolium*: culture 204, Florida, open marsh with about 40 individuals, Collier Co., 0.7 mile south of state route 92 on U.S. Highway 41, about 3.5 miles inland from coast; *Ceratopteris thalictroides*: culture 174, Guyana, two miles east of Georgetown on main coastal public road, in wet marsh with *Nymphaea* next to gasoline station; culture Hawaii, taro patches, Hawaiian Islands, inundated weekly with fresh water. Adscript numbers and letters designate spore progenies from different individual sporophytes collected at each location.

Spores were sown and gametophytes grown on inorganic nutrient medium solidified with 1% agar (see Klekowski 1969, for composition) in 100 x 15mm petri dishes under continuous illumination from fluorescent and incandescent lamps at about 23°C. Nutrient media were supplemented with NaCl prior to the addition of agar, yielding concentrations of 0.5 to 3.0%. NaCl concentration was ascertained by conductivity measurements (from 0.8mmhos/cm at 25°C in control to 44mmhos/cm in 3.0% NaCl.) Conductivity was measured with a Radiometer CDM2 conductivity meter. Data for 190-D/193-B (Table 4) represent gametophytes of both progenies transferred on to single petri dishes.

TABLE 1

Percent spore germination in *Acrostichum* (15 days following sowing) and *Ceratopteris* (12 days following sowing) at salinity regimes varying from 0.0% to 3.0% NaCl. (Sample size = 100).

Species and Culture Number								
	<i>A. aureum</i>			<i>A. danaeifolium</i>		<i>C. thalictroides</i>		
NaCl (%)	190-D	193-B	193-K	204-2	204-8	174-A	Hawaii-A	Hawaii-B
0.0	69(100*)	66(96)	76(100)	99	89(100)	86(96)	95(100)	90(100)
0.5	55(80)	69(100)	61(80)	99	67(75)	90(100)	50(52)	20(22)
1.0	51(74)	60(87)	47(62)	92	72(81)	85(94)	30(32)	0
1.25	19(28)	44(64)	54(71)	72	54(61)	84(93)	0	0
1.5	11(16)	43(62)	56(74)	24	21(24)	19(21)	0	0
1.75	3(4)	19(28)	17(22)	28	8(9)	11(12)	0	0
2.0	1(1.4)	8(12)	17(22)	18	1(1)	2(2.2)	0	0
2.25	2(3)	2(3)	5(7)	3	0	0	0	0
2.5	0	1(1.4)	4(5)	0	0	0	0	0
2.75	0	0	1(1.3)	0	0	0	0	0
3.0	0	1(1.4)	1(1.3)	0	0	0	0	0

*Values given in () are adjusted to 100% to adjust for variation in intersporophytic spore viability.

RESULTS

Spore germination in all three species initially occurred five to six days following sowing and was highest in the control and the lowest NaCl concentration. There was a differential response of spore progenies from individual sporophytes of each species to each of the culture regimes. In *Acrostichum*, germination rates differ slightly at the higher NaCl concentrations (Table 1). Spore progenies of both species exhibited consistent but decreasing levels of germination up to 1.25% NaCl. At salinities above 1.25 and 1.5%, respectively, in *A. danaeifolium* and *A. aureum*, there are significant decreases in germination. At NaCl concentrations between 2.25 and 3.0%, spore progenies of *A. aureum* exhibited low levels of germination, whereas in the other species germination did not occur. There are indications of bimodality (stress pulses) in three of the five dose response curves (193-K, 204-2, 204-8 at salinities of 1.25-1.5%, 1.75%, and 1.0% respectively). If this pattern is real it could result from the operation of two physiological processes whose reaction optima occur at different levels of salinity.

In *Ceratopteris*, germination was greatly inhibited in Hawaiian spore progenies at all NaCl concentrations and did not occur above 1.0%. The Guyana sample is of potential interest, however, as germination responses were similar to those of *A. danaeifolium*.

The fraction of gametophytes to attain two-dimensional growth within 15 days of sowing was determined in order to evaluate the effect of salinity on developmental rates (Table 2). There is no appreciable difference in the two species of *Acrostichum* at the lower salinities with almost all gametophytes reaching the two-dimensional stage. The reaction curves for developmental rate versus salinity are markedly bimodal for the spore progenies of *A. aureum* tested. Developmental rates decreased synchronously for all four samples from both species between 1.0 and 1.25% NaCl. The second range of salinities (1.25 to 1.75%) which resulted in rapid gametophyte development for *A. aureum* produced reduced development in culture 204-2 and severely inhibited development at 1.75% NaCl in culture 204-8 of *A. danaeifolium*. The phenomenon responsible for the higher developmental rate in higher salinities for *A. aureum* appears to extend this species' maximum salinity tolerance beyond that of *A. danaeifolium*. However, it was not determined what proportion of 15 day old one-dimensional gametophytes later attained the two-dimensional stage under hypersalinity conditions.

TABLE 2

Mean percent attainment of two-dimensional morphology in gametophytes of *Acrostichum* grown under varying salinity regimes 15 days following sowing.

NaCl (%)	Species and Culture Number			
	<i>A. aureum</i>		<i>A. danaeifolium</i>	
	193-B	193-K	204-2	204-8
0.0	100	97	100	100
0.5	100	96	100	100
1.0	100	97	97	98
1.25	90	84	85	93
1.5	97	90	80	87
1.75	97	86	83	14
2.0	75	54	0	0
2.25	0	0	0	0

Sample size variable and dependent upon number of available gametophytes: 30-45 in 0.0% to 1.75%; (1)10-29 in 2.00%; 11-14 in 2.25%; less than 5 in remaining regimes.

TABLE 3

Maximum and (mean) gametophyte size (in sq. mm) attained in cultures of *Acrostichum* at salinity regimes varying from 0.0% to 2.25%. Sample size = 10.

Species and Culture Number						
<i>A. aureum</i>		<i>A. danaeifolium</i>				
NaCl (%)	190-D*	193-B*	193-K**	204-2***	204-8***	
0.0	2.8(1.4)	10.9(3.8)	4.1(2.4)	11.8(5.1)	6.3(4.3)	
0.5	1.9(1.0)	5.9(2.8)	13.9(2.0)	6.0(3.1)	8.5(3.2)	
1.0	2.0(0.9)	4.0(1.8)	4.5(2.0)	4.0(2.1)	2.8(1.2)	
1.25	0.4(0.3)	2.5(1.2)	1.8(0.8)	2.4(1.2)	1.9(0.9)	
1.5	1.1(0.6)	1.2(0.7)	0.4(0.2)	0.7(0.4)	0.8(0.4)	
1.75	-----	0.6(0.4)	0.4(0.4)	-----	0.09(0.08)	
2.0	-----	0.1(0.1)	0.2(0.1)	-----	-----	
2.25	-----	0.2(0.1)	0.09(0.07)	-----	-----	

* sampled 19 days following sowing.

** sampled 18 days following sowing.

*** sampled 21 days following sowing.

TABLE 4

Mean percent non-chlorotic tissue in gametophytes of *A. aureum* grown 70 days in nutrient control medium and then transferred to variable salinity regimes.

NaCl (%)	150-B: Days from transfer			190-D/193-B: Days from transfer		
	3	14	21	4	7	15
0.0	99	91	91	100	100	100
1.0	100	99	99	100	100	100
1.25	94	86	94	100	99	92
1.75	91	80	83	97	91	69
2.0	71	74	75	97	90	72
2.25	73	62	58	87	74	69
2.5	40	27	0	76	81	39
2.75	45	31	0	38	25	13
3.0	40	30	0	32	23	0

Maximum and mean gametophyte area was measured 18 to 21 days following sowing to evaluate the effect of salinity on growth rates (Table 3). The growth rate of *A. danaeifolium* appears to be greatest in the 0% NaCl controls and then decreases linearly with increasing levels of salinity. Low NaCl concentrations (0.5 and 1.0%) reduced growth rates of *A. danaeifolium* to a greater extent than those of *A. aureum*. For example, reduction of mean gametophyte size (compared to 0.0% NaCl) of *A. aureum* progenies varies from 16.7 to 52.7%, whereas reduction in size of *A. danaeifolium* progenies is 58.9 to 72.1%.

Salt stress and development of chlorotic tissue was measured in gametophytes of *A. aureum* (Table 4). These gametophytes were grown to maturity for 70 days on control media and then transferred to various salinity regimes. In culture 150B, below 2.0% NaCl there is no apparent difference over time but only with salinity concentration. The effect appears to be initial and then persistent. There is some indication of a stress pulse at 1.25 to 2.0% NaCl with gametophytic tissue recovery after 21 days. Above 2.25%, the salinity effects are progressive over time. In culture 190/193, effects appear to be absent below 1.25% NaCl. At levels of 1.25% and above, there is a progressive increase in chlorotic gametophytic tissue with both time and NaCl concentration.

DISCUSSION

The tolerance to salinity of gametophytes of both species of *Acrostichum* appears to be significantly greater than two of the three progenies of the glycophyte *Ceratopteris thalictroides*. Warne and Hickok (pers. comm.) have also studied NaCl effects on spore progenies of *C. thalictroides*. They analyzed spore germination and gametophyte survival of progenies from ten sporophytes from various parts of the World. These progenies exhibit a wide range of tolerance to NaCl. At 0.8% NaCl, spore germination in six of the ten progenies was reduced by 4.0 to 15.9 (mean = 7.53%) compared to the controls (0.0% NaCl). In the remaining four progenies, germination was reduced 48.8 to 97.3 (mean = 77.7)%. Twenty-one days following sowing, gametophytes of the former group were 2.5 to 10% the size of control gametophytes, whereas gametophytes of the latter group failed to survive. These results indicate that some populations of *Ceratopteris* may have salinity tolerance approaching that exhibited by *A. danaeifolium*. Recently, Petersen (1985) reported that spores of *A. danaeifolium* were capable of germinating in up to 2.5% NaCl whereas spores of the glycophytic species *Osmunda* spp. and *Onoclea sensibilis* ceased germination at 0.6% NaCl.

In *Acrostichum*, there is a wide range of tolerance to salinity, although *A. aureum* consistently shows a slightly greater tolerance at slightly higher NaCl levels. In spore germination, two of the three progeny samples of *A. aureum* show 50% germination at NaCl concentrations of 1.5 and 1.75%. In *A. danaeifolium*, 50% germination occurs between 1.25 and 1.5%. Similarly, the critical salinity level for attainment of two-dimensional morphology is 1.75 to 2.0% NaCl in *A. aureum* and 1.5 to 1.75% in *A. danaeifolium*. In addition, some progenies of mature gametophytes of *A. aureum* can tolerate prolonged exposure to salinities of 2.0 to 2.25%. These results suggest that the critical soil salinity which will limit gametophyte survival of *A. danaeifolium* will be about 1.5% and of some plants of *A. aureum*, about 1.75 to 2.0%. However, due to the extremely large number of spores produced by individual sporophytes of these species, even very low percentages of survival at higher salinities could result in millions of successful gametophytes.

Germination and growth in *Acrostichum* parallels that of other mangrove species which have been studied and have optimal growth between 0.6 and 1.5% NaCl (Connor 1969; Pannier 1959; Patil 1964).

The spore germination and gametophyte growth patterns of *A. danaeifolium* are similar to those described for semi-halophytes by Waisel (1972). Semi-halophytes show a slow decrease in growth at initial stages of salinity increase, followed by a steady decrease with increasing salinity. On the other hand, in *A. aureum*, the stress-pulse growth phases followed by a steady decrease in growth with increasing salinities is similar to the pattern of true halophytes. These studies indicate, therefore, that species of *Acrostichum* can be considered to be semi-halophytes or halophytes and that the salinity tolerance by the gametophyte generation is an integral part of their life-history.

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THE ECOLOGY OF PTERIDOPHYTES IN THE MWANIHANA FOREST RESERVE, TANZANIA

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ABSTRACT

A collection of pteridophytes made in the Mwanihana Forest Reserve, Tanzania is described and related to the ecology of the forest. In all 78 species were collected, demonstrating the richness of the area in comparison with the total number of 500 species estimated for the whole of tropical Africa.

INTRODUCTION

The Mwanihana Forest Reserve (7°50'S 36°55'E) is located on the steep east facing escarpment of the Uzungwa Mts, overlooking the Kilombero Valley and Selous Game Reserve. These mountains are composed of Pre-Cambrian crystalline gneiss, and have probably been in existence since the Cretaceous. The rainfall is relatively high for Tanzania, being estimated to be 2,000-2,500mm a year with one wet season receiving greater than 100mm of rain a month between November and May on average, which has a peak in March and April (DHV, 1982). The dry season, between July and October, receives less than 50mm of monthly rain on average, with months of no rain common.

Despite the marked dry season the escarpment is covered by continuous closed moist forest from an altitude of 450m to 1,800m, and in the past extended into the Kilombero flood plain where it has now been replaced by sugar plantation. These forests are part of the Eastern Arc group (Lovett, in press) which are notable for the high degree of endemism they contain, and it is now hoped that the Mwanihana Forest Reserve will become a National Park in order to protect many rare plants and animals.

During the course of surveying the Reserve as part of the 1984 Uzungwa expedition supported by the National Geographic Society and World Wildlife Fund, a substantial collection of plants was made. This collection included some 78 species of pteridophytes from the Mwanihana and nearby forest reserves which are presented here divided into various ecological categories, and as a check-list. The collections made were far from exhaustive, and there are probably something in the region of 100 species of pteridophyte in the area. This is high for Tropical Africa, which is estimated to contain only 500 species altogether (Parris, 1985). Thus the small area of the Mwanihana Forest Reserve may contain as much as 20% of the total Tropical African pteridophyte flora.

Despite the incompleteness of the collections and the brief nature of the ecological observations it was thought necessary to publish them in order to draw attention to the high species richness of the Mwanihana Forest Reserve in the hope that further work may be stimulated.

ECOLOGY

The vegetation of Africa has been divided into a number of phytocoria based on plant species distribution and physiognomic types which are described by White (1983). Although the broad scope of this work renders it inaccurate at the small scale, it is useful as a general pattern within which to designate arbitrary ecological boundaries. Five types of forest can be recognised in the Mwanihana Forest Reserve according to this system, and they are briefly described below for the forest reserve using White's terminology. Ten examples of tree species which occur in each forest type in the reserve are also given.

Within each forest type the pteridophyte habitat is divided into terrestrial, lithophytic, and epiphytic. Additional notes on the habitat follow the species name in parenthesis when necessary. All pteridophytes were growing in forest shade unless noted. These notes are self explanatory except for the following: an exposed habitat is one in partial shade; a stream habitat is on rocks in streams and river beds flowing through the forest. A "C" in parenthesis indicates that the species was collected at Chita (8° 30' S 35° 55' E), a locality to the south of the reserve, but also in the Uzungwa mountains. All other species were collected in the reserve.

Zanzibar-Inhambane Lowland Forest

Altitudinal range 450-750m, canopy height 25-30m with emergents to 40m. Large trees include: *Afrosersalisia cerasifera*; *Albizia adianthifolia*; *Aningeria pseudoracemosa*; *Chlorophora excelsa*; *Dialium holtzii*; *Erythrophleum suaveolens*; *Funtumia africana*; *Lettowianthus stellatus*; *Newtonia paucijuga*; *Terminalia sambesica*. Terrestrial: *Bolbitis acrostichoides*, (C)*; *Christella hispidula*, (C); *Microlepia speluncae*; *Pellaea doniana*, (exposed).

Lithophytic: *Adiantum capillus-veneris*, (exposed); *Bolbitis* sp. aff. *acrostichoides*, (C); *Nephrolepis biserrata*, (C).

Zanzibar-Inhambane Intermediate Forest

Altitudinal range 750-1,200m, canopy height 25-30m with emergents to 40m. Large trees include: *Anisophylla obtusifolia*; *Cassia angolensis*; *Cephalosphaera usambarensis*; *Ochna holstii*; *Octoknema orientalis*; *Sibangea pleioneura*; *Syzygium guineense*; *Tabernaemontana holstii*; *Trichilia dregeana*; *Uapaca pallidosa*. Terrestrial: *Amphineuron opulentum*; *Asplenium blastophorum*; *A. obscurum*, (C); *Bolbitis auriculata*; *B. gemmifera*; *Christella gueintziana*, (C) (swamp); *Lonchitis occidentalis*; *Pteris* sp. aff. *mildbraedii*; *P.* sp. aff. *prolifera*; *P. quadriaurita* subsp. *friesii*; *Tectaria gemmifera*.

Lithophytic: *Antrophyum mannianum*, (C) (stream); *Asplenium formosum*, (stream); *A. inaequilaterale*; *A. unilaterale*; *Bolbitis* sp. aff. *acrostichoides*; *Christella* sp. aff. *gueintziana*, (stream); *Elaphoglossum spathulatum*, (stream); *Menisorus pauciflorus*, (stream); *Sphaerostephanos arbuscula* subsp. *africanus*, (stream).

Epiphytic: *Lycopodium phlegmaria*, (canopy).

Afromontane Rain-Forest

Altitudinal range 1,200-1,700m, canopy height 25-30m, with emergents to 35m. Large trees include: *Allanblackia stuhlmannii*; *Beilschmiedia kweo*; *Cassipourea gummiflua*; *Cleistanthus polystachyus*; *Chrysophyllum gorungosanum*; *Myrianthus holstii*; *Newtonia buchananii*; *Ocotea kenyensis*; *Parinari excelsa*; *Strombosia scheffleri*.

Terrestrial: *Asplenium christii*; *A.* sp. aff. *gilpinae*; *A. hypomelas*; *A. monanthes*; *A. volkensii*; *Athyrium scandicinum*; *Blechnum attenuatum*; *B. ivohibense*; *Blotiella natalensis*; *Ctenitis languinosa*; *Cyathea humilis*, (ravine); *Cyathea mossambicensis*; *Didymochlaena trunculata*; *Diplazium nemorale*; *D. pseudoporrectum*; *Dryopteris inaequalis*; *D. kilemensis*; *Histiopteris incisa*; *Microlepia fadenii*; *Polystichum zambesiaceum*; *Pneumatopteris usambarensis*; *Pteris buchananii*; *P. preussii*; *P. pteridioides*; *Tectaria gemmifera*; *Trichomanes cupressioides*; *T. giganteum*.

Lithophytic: *Asplenium boltonii*, (damp, exposed); *Elaphoglossum phanerophlebium*; *Hymenophyllum splendidum*; *Pellaea angulosa*; *Trichomanes borbonicum*.

Epiphytic: *Asplenium aethiopicum*; *A. dregeanum*; *A. rutifolium*; *Belvisia spicata*; *Elaphoglossum acrostichoides*; *Hymenophyllum polyanthos* var. *kuhnii*; *H. sibthorpioides*; *H. splendidum*; *Lomariopsis warneckei*; *Lycopodium verticillatum*; *Trichomanes giganteum*.

* = collected at Chita (see text above).

Afromontane Undifferentiated Forest

Altitudinal range 1,200-1,800m, canopy height 15-25m. This forest type represents a drier or more exposed type of Afromontane Rain-Forest. Large trees include: *Aphloia theriformis*; *Bequaetiodendron magalismontanum*; *Cryptocaria liebertiana*; *Ficalhoa laurifolia*; *Hirtella megacarpa*; *Isoberlinia scheffleri*; *Psydrax vulgare* subsp. *rubrocristatum*; *Rapanea melanophloeos*; *Xylopia aethiopica*; *Xymalos monospora*. Terrestrial: *Schizaea dichotoma*; *Dicranopteris linearis*, (exposed).

Afromontane evergreen bushland and thicket

Altitudinal range 1,700-1,800m, canopy height 5-10m. In the reserve this forest type is better referred to as Elfin Forest, and has been described for the nearby Uluguru mountains by Pocs (1976). It is a variant of Afromontane undifferentiated forest but is distinguished by the low canopy and rich cover of epiphytic bryophytes, indicating that a great deal of moisture must come from mist. Large trees include: *Allanblackia ulugurensis*; *Apodytes dimidiata*; *Faurea saligna*; *Maytenus acuminata*; *Ocotea usambarensis*; *Olinia rochetiana*; *Podocarpus latifolius*; *Syzygium cordatum*; *Ternstroemia polypetala*; *Trichocladus goetzei*.

Terrestrial: *Blechnum punctulatum*.

Lithophytic: *Elaphoglossum macropodium*.

Epiphytic: *Ctenopteris* sp. aff. *villosissima*; *Elaphoglossum macropodium*; *Grammitis kymbilensis*; *G. nanodes*; *Lycopodium ophioglossoides*; *L. dacrydioides*; *Pleopeltis excavata*; *Xiphopteris strangeana*.

Collection List

The following is a list of the pteridophyte collections made in the Mwanihana Forest Reserve and Chita forests of the Uzungwa scarp. The numbers are those of D.W. Thomas' collections. The collection is at MO, with duplicates at DSM and K. All the species mentioned in this list are also cited in the ecology section of this paper.

Pteridophyta**Filicopsida****Adiantaceae**

Adiantum capillus-veneris L., 3933

Pellaea angulosa (Bory ex Willd.) Bak., 3861

P. doniana J. Sm. ex Hook., 3934

Aspidiaceae

Ctenitis lanuginosa (Willd. ex Kaulf.) Copel., 3862

Didymochlaena trunculata (Sw.) J. Sm., 3918

Dryopteris inaequalis (Schlechtend.) Kuntze var. *inaequalis*, 3802, 3881

D. kilemensis (Kuhn) Kuntze, 3880

Tectaria gemmifera (Fée) Alston, 3685, 3895

Polystichum zambesiaceum Schelpe, 3801, 3925

Aspleniaceae

Asplenium aethiopicum (Burm. f.) Becherer, 3923

A. blastophorum Hieron., 3688

A. boltonii Hook. ex Schelpe, 3878

A. christii Hieron., 3676

A. dregeanum Kunze, 3856

A. formosum Willd., 3696

A. hypomelas Kuhn, 3885

A. inaequilaterale Willd., 3697

A. monanthes L., 3855, 3858

A. obscurum Bl., 3955

A. rutifolium (Berg.) Kunze, 3854

- A. unilaterale* Lam., 3686
A. ?volkensii Hieron., 3883
A. sp. aff. gilpiniae Bak., 3919

Athyriaceae

- Athyrium scandicinum* (Willd.) C. Presl, 3864
Diplazium nemorale (Bak.) Schelpe, 3863, 3917
D. pseudoporrectum Hieron., 3857

Blechnaceae

- Blechnum attenuatum* (Sw.) Mett., 3891
B. ivohibense C. Chr., 3884
B. punctulatum Sw., 3813

Cyatheaceae

- Cyathea humilis* Hieron., 3886
C. mossambicensis Bak., 3889

Davalliaceae

- Nephrolepis biserrata* (Sw.) Schott, 3974

Dennstaedtiaceae

- Blotiella natalensis* (Hook.) Tryon, 3675
Histiopteris incisa (Thunb.) J. Sm., 3859
Lonchitis occidentalis Bak., 3683
Microlepia fadenii Pic. Ser., 3869
M. speluncae (L.) Moore, 3932

Gleicheniaceae

- Dicranopteris linearis* (Burm. f.) Underw., 3709

Grammitidaceae

- Ctenopteris sp. aff. villosissima* (Hook.) Harley, 3815
Grammitis kyimbilensis (Brause) Copel., 3817A
G. nanodes (A. Peter) Ching, 3817
Xiphopteris strangeana Pic. Ser., 3818, 3847A

Hymenophyllaceae

- Hymenophyllum polyanthos* Sw. var. *kuhnii* (C. Chr.) Schelpe, 3866
H. sibthorpioides (Bory ex Willd.) Mett. ex Kuhn, 3865
H. splendendum v.d. Bosch, 3867
Trichomanes borbonicum v.d. Bosch, 3868
T. cupressoides Desv., 3681
T. giganteum Bory ex Willd., 3682

Lomariopsidaceae

- Bolbitis acrostichoides* (Swartz) Ching, 3972
B. auriculata (Lam.) Alston, 3661
B. gemmifera (Hieron.) C. Chr., 3742A
B. sp. aff. acrostichoides (Swartz) Ching, 3658, 3659, 3973
Elaphoglossum acrostichoides (Hook. & Grev.) Schelpe, 3821
E. macropodium (Fée) Moore, 3814
E. phanerophlebium C. Chr., 3849
E. spathulatum (Bory) Moore, 3659A
Lomariopsis warneckei (Hieron.) Alston, 3890

Polypodiaceae

- Belvisia spicata* (L.f.) Mirb., 3814A
Pleopeltis excavata (Bory ex Willd.) Sledge, 3816

Pteridaceae

- Pteris buchananii* Bak. ex Sim, 3887
P. preussii Hieron., 3888
P. pteridioides (Hook.) Ballard, 3860
P. quadriaurita Retz. spp. *friesii* (Hieron.) Schelpe, 3689

- P. sp. aff. mildbraedii/atrovirens*, 3695
P. sp. aff. prolifera Hieron, 3742

Schizaeaceae

Schizaea dichotoma (L.) Smith, 3699

Thelypteridaceae

- Amphineuron opulentum* (Kaulf.) Holtt., 3743
Christella gueintziana (Mett.) Holtt., 3946
C. hispidula (Decne) Holtt., 3971
C. sp. aff. gueintziana (Mett.) Holtt., 3694
Menisorus pauciflorus (Hook.) Alston, 3655
Sphaerostephanos arbuscula (Willd.) Holtt. ssp. *africanus* Holtt., 3693
Pneumatopteris usambarensis Holtt., 3920

Vittariaceae

Antrophyum mannianum Hook., 3945

Lycopsidea

Lycopodiaceae

- L. dacrydioides* Bak., 3807
L. ophioglossoides Lam., 3765
L. phlegmaria L., 3654
L. verticillatum L.f., 3808

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We gratefully acknowledge the assistance of Dr B.S. Parris of the Royal Botanic Gardens, Kew, in naming the fern collection. The Tanzanian National Scientific Research Council and Ministry of Natural Resources and Tourism very kindly gave us permission to work in the Mwanihana Forest Reserve. The National Geographic Society and World Wildlife Fund generously supported the field work. Langson Kusoma and Henry provided much needed assistance in the field.

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REVIEW

INDEX FILICUM – SUPPLEMENTUM QUINTUM PRO ANNIS 1961-1975 by F.M. Jarrett, with T.A. Bence, J.W. Grimes, B.S. Parris and J.L.M. Pinner. Pp. 245. Clarendon Press, Oxford. 1985. ISBN 0-19-854579-7. Price £25.00.

Fern taxonomists have been well served by the provision of Indices giving the details of the publication of names. *Index Filicum* (1905-1906) was compiled by Carl Christensen who updated it by producing Supplements in 1913, 1917 and 1934. This valuable work was continued by a committee of I.A.P.T. who published in 1965 the Fourth Supplement covering the period from 1934 to 1960.

The present Fifth Supplement has been compiled at Kew under the direction of Dr Frances Jarrett who undertook the onerous task of extracting names from the literature from 1961 to 1970, this being continued by her collaborators to complete the period covered by this work.

The Supplement lists new names at all ranks between family and species but does not make taxonomic judgements as did Christensen's work. Infra-specific categories are not included as a general rule although they are quoted where they form the basionym for a new name. Where hybrids have been named their parentage is given and cross-referenced, for example *Dryopteris x gotenbaensis* Nakaike is quoted in full together with the information that it is the hybrid of *D. hondoensis x uniformis*. A further entry for *D. hondoensis x uniformis* refers the reader to the name *D. x gotenbaensis*. Thus, having either the name of the hybrid or its parentage the other can be found — a very useful feature when it increasingly is becoming common practice to give formal names to hybrids.

All previous parts of the *Index* have dealt exclusively with ferns, a somewhat restrictive practice as fern workers are usually involved with the pteridophytes as a whole. Compilations of names for the fern allies have appeared in a variety of places at different times and it is a great convenience for them to be included along with the ferns as has been done in this Fifth Supplement for the first time.

Users of the *Index* owe a great debt to the compilers for the meticulous way in which the work has been carried out. The publishers are also to be congratulated on the overall presentation and the quality of the type face.

T.G. WALKER

GEORGE GARDNER'S PTERIDOPHYTE HERBARIUM AND LECTOTYPES OF GARDNER'S NEW FERN SPECIES

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ABSTRACT

George Gardner's original pteridophyte collections are at CGE and not with his phanerogam material (Brazilian specimens at BM, Ceylon specimens at K).

INTRODUCTION

George Gardner (1812-1849) is well-known as a botanical explorer in Brazil who later became superintendent of the Peradeniya Botanic Garden in Ceylon. His collections from both countries are large and important. The originals of his Brazilian material are stated to be in the British Museum (Natural History) (BM), while those of his Ceylon plants are said to be in the herbarium of the Royal Botanic Gardens, Kew (K) (Stafleu & Cowan 1976). These were presumably part of the herbarium offered for sale by Samuel Stevens and described in the *Gardeners' Chronicle* of 31st May 1851 (Anon. 1851). The disposition of Gardner's higher plants is undoubtedly as given above, but it is not so for the pteridophytes. Although both BM and K hold good sets of his pteridophyte numbers they are all duplicates and the original collections are held in the herbarium of the Botany School, University of Cambridge (CGE).

A clue to how this may have come about is provided by a small printed label attached to some of the sheets which reads "Presented by Dr Churchill Babington". Dr Babington is known to have had an interest in cryptogams and presumably purchased the pteridophyte part of Gardner's collections either directly or indirectly from Samuel Stevens for his own use. In 1865 he became Professor of Archaeology at the University of Cambridge. At that time his cousin Charles Cardale Babington was Professor of Botany at Cambridge (Desmond 1977) and was acquiring duplicates of the major plant collections then available for the University Herbarium; doubtless Churchill Babington presented them to the Botany School as a gift to the herbarium which was rapidly expanding under his cousin's administration.

The c. 1990 sheets of Gardner's material are mounted on a distinctive blue lined paper and include not only his own gatherings but also duplicates from a variety of other collectors. I propose to document the latter in a subsequent paper. His own numbered original collections are represented, together with many un-numbered sheets which were presumably unicates or plants collected in too small a quantity to be numbered and distributed as duplicates. These are from Brazil, British Isles, Ceylon, India and Mauritius. None of the sheets of his own collections bear his name, but the handwriting is undoubtedly Gardner's and matches exactly that on his duplicates and in his notebooks kept at CGE, and the names and numbers on the duplicates (of which there are four incomplete sets in CGE) always correspond with those of the originals. The duplicates are widespread in herbaria (Stafleu & Cowan 1976) and usually have the plant name and number written in Gardner's hand; sometimes locality and date of collection is indicated, but ecological information is lacking. This is often present on the originals and is usually quoted verbatim in his descriptions of new species.

Gardner described 16 new species of fern and now that his original pteridophyte collections have come to light (with the exception of one type) it seems expedient to choose lectotypes for them.

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The lectotypes of George Gardner's fern species at CGE.

Information in quotation marks is written in Gardner's hand on the herbarium sheets.

Acrostichum alpestre Gardner

in Fielding & Gardner, *Sert.Pl.* t.25 (1844).

[Gardner] "5924. On shady rocks near the summit of the Organ Mountains. March 1841.

Acrostichum alpestre, Gardn."

Lectotype chosen here.

Adiantum filiforme Gardner

in Hooker, *lc.Pl.* t.503 (1843).

[Gardner] "2391. Shady cliffs of sandstone rocks. Oeiras, Piauhý. 1839.

Adiantum filiforme, Gardn."

Lectotype and 3 isoelectotypes chosen here.

Adiantum sinuosum Gardner

in Hooker, *lc.Pl.* t.504 (1843).

[Gardner] "3552. Serra de Natividade. Goyaz, Brazil. Jany. 1839.

Adiantum sinuosum, Gardn."

Lectotype and 3 isoelectotypes chosen here.

Anemia dentata Gardner

in Fielding & Gardner, *Sert.Pl.* ad t.70 (1844).

[Gardner] "2387. Between Canabrava & Tranquiera, Province of Piauhý, Brazil. 1839.

Anemia dentata, Gardn."

Lectotype and 3 isoelectotypes chosen here.

Anemia glareosa Gardner

in Fielding & Gardner, *Sert.Pl.* t.70 (1844).

[Gardner] "4086. Dry open campos, Goyaz, Brazil. Near Natividade and Arrayas. 1840.

Anemia glareosa, Gardn."

Lectotype and 2 isoelectotypes chosen here.

Anemia pallida Gardner

in Fielding & Gardner, *Sert.Pl.* ad t.70 (1844).

[Gardner] "3560 bis. On rocks in woods. Natividade, Goyaz. Jany. 1840.

Anemia pallida, Gardn."

Lectotype and 2 isoelectotypes chosen here.

Anemia wightiana Gardner

in *Calcutta Jour.Nat.Hist.* 7:10, t.1-2 (1847).

[Gardner s.n.]

"Open rocky places on the Malabar slopes of the Neelgherries. Feby. 1845.

Anemia wightiana. Gardner in *Calcutta Journ.*"

Lectotype and isoelectotype chosen here.

Asplenium woodwardioideum Gardner

in *Lond.Jour.Bot.(Hooker)* 1:547 (1842).

[Gardner] "43. Corcovado, Rio de Janeiro. 1836.

Asplenium woodwardioideum, Gardn."

Lectotype chosen here.

Cassebeera gleichenioides Gardner

in Hooker, *lc.Pl.* t.507 (1843).

[Gardner] "5295. Bushy rocky places. Diamond district. Aug. 1840.

Cassebeera gleichenioides, Gardn."

Lectotype and 2 isoelectotypes chosen here.

Cheilanthes monticola Gardner

in Hooker, *lc.Pl.* t.487 (1842).

[Gardner] "3557. Summit of the Serra de Natividade. Province of Goyaz. Brazil. Jany. 1840.

Cheilanthes monticola, Gardn."

Lectotype and 3 isoelectotypes chosen here.

Coptophyllum buniifolium Gardner

in *Lond. Jour. Bot. (Hooker)* 1:133 (Jan. 1842).

[Gardner] "4084. Serra de Natividade, Goyaz, Brazil, 1840.

Coptophyllum buniifolium, Gardn."

Lectotype and 3 isoelectotypes chosen here.

Coptophyllum millefolium Gardner

in *Lond. Jour. Bot. (Hooker)* 1: 133 (Jan. 1842).

[Gardner] "4083. Villa de Arrayas, Goyaz, Brazil, 1840.

Coptophyllum millefolium, Gardn."

Lectotype and 4 isoelectotypes chosen here.

Grammitis organensis Gardner

in Hooker, *lc. Pl.* t.509 (1843).

[Gardner] "5913. On rocks and on the stems of trees near the summit of the Organ Mountains, March. 1841.

Grammitis organensis, Gardn."

Lectotype and 2 isoelectotypes chosen here.

Polystichum pallidum Gardner

in *Lond. Jour. Bot. (Hooker)*: 1:547 (1842).

[Gardner] "54. Woods, Corcovado, Rio de Janeiro, 1836.

Polystichum pallidum, Gardn."

Lectotype chosen here.

Trochopteris elegans Gardner

in *Lond. Jour. Bot. (Hooker)* 1:74 (Jan. 1842).

[Gardner] "4085. Serra de Natividade, Goyaz, Brazil. Feby. 1840.

Trochopteris elegans, Gardn."

Lectotype and 3 isoelectotypes chosen here.

Only one species described by Gardner is not lectotypified here. *Adiantum calcareum* Gardner in Hooker, *lc. Pl.* t.467 (1842) was based on Gardner no. 3551, but there is no original material of this number at present in CGE. Although duplicates exist (two of them in CGE) it is possible that the original may yet be found at CGE and typification should ideally wait until then.

ACKNOWLEDGEMENTS

I am grateful to Peter Sell, Assistant Curator of the herbarium, Botany School, Cambridge, for his advice and encouragement during my studies on the pteridophyte collections in CGE.

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REVIEW

ILLUSTRIERTE FLORA VON MITTELEUROPA/GUSTAV HEGI Bd I Teil I PTERIDOPHYTA, 3rd fully revised edition by Karl U. Kramer. 309 pp., 11 coloured plates, 275 figs. 200 x 268mm. Paul Parey, Berlin & Hamburg. ISBN 3-489-500020-2. Price DM 228. (1984). (Publ. 1983).

Our concepts in species delimitations, distribution and general systematic relationships in Pteridophyta have changed considerably over the last 35 years and so this completely rewritten work (by J. Dostal, T. Reichstein, C.R. Fraser-Jenkins & K.U. Kramer) of this classic regional Flora, previously produced in 1935, is long overdue and greatly welcomed. Geographically the area of the Flora (shown in map-form on the end papers) is difficult to equate with present-day political boundaries, being originally based on the German and Austrian Empires with the addition of Switzerland. Thus Alsace-Lorraine (France), Slovenija (Yugoslavia), Bohemia/Moravia (Czechoslovakia), Posen and Prussia (Poland) are included. This is hardly a floristic zone and one could ask why not include the whole of Poland and Czechoslovakia — and also Hungary?

After a brief but concise general account of the group the book describes 39 genera in 23 families. Comprehensive and detailed descriptions of genera and species are illustrated with line drawings and/or silhouettes and photographs of the plants in situ. Most species are shown in the eleven excellent coloured plates. At the taxonomic level, full synonymy, with references, and infra-specific variation is given; ecology, with associated species and both general (with maps) and detailed (in the area of the Flora) distribution is discussed. Vernacular names, including English, are also listed as are many relevant references to all chapters and subheads. Hybrids are treated less fully but still in considerable detail.

A comprehensive work such as this, written by experts and edited with such thoroughness by Karl Kramer is, of course, a mile-stone in regional Floras. It will also be used as a reference book in a wider context e.g. for guidance to family names and classification. At this level it would have been useful to give synonymy of family names and a little discussion. In the reviewer's opinion the names and concepts used are sound and I hope that they will be taken up by other forthcoming European Floras.

One cannot fault a book like this except on minor points. The illustrations vary: some are precise and pertinent e.g. in *Polystichum*; others not so helpful, e.g. the line drawings of *Diphasiastrum* do not show as much as the photographs and could have shown the important differences in lower leaves. Professor Kramer's eagle eye has eliminated even small errors but I noticed, under *Ophioglossum azoricum*, *O. vulgatum* subsp. *ambiguum* (Cross. et Germ.) E.F. Warburg being quoted as published in C.T.W. Fl. Brit. Isles (1962). Warburg published the combination in *Watsonia* 4: 41 (1957). Much more unfortunate is the use of often unclear light microscope photographs of spores when surely SEM pictures would have said everything, and on Plate 5 the individual figures are incorrectly labelled in relation to the key on p.160.

A.C. JERMY

A NEW *DRYOPTERIS* HYBRID FROM SPAIN

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ABSTRACT

A new *Dryopteris* hybrid, *D. x asturiensis* Fraser-Jenkins & Gibby, is described, and the cytology of this hybrid and *D. corleyi* Fraser-Jenkins is discussed.

The northern coastal region of Spain is particularly rich in *Dryopteris* species, including the recently described endemic *D. corleyi* Fraser-Jenkins (1983) and *D. guanchica* Gibby & Jermy, known only from the Iberian peninsula and the Canary Islands, and thus provides opportunities for hybridization. A recently discovered hybrid from this area is *D. x fraser-jenkinsii* Gibby & Widén (1983), the hybrid between *D. affinis* (Lowe) Fraser-Jenkins subsp. *affinis* and probably *D. guanchica*, although the second parent could possibly be *D. dilatata* (Hoffm.) Gray. A second hybrid involving *D. affinis* has been found in N Spain recently, and although similar in morphology to *D. x fraser-jenkinsii*, differs in certain characters, and particularly in its cytology. Both hybrids are tetraploid, and produce some 8-celled sporangia with 164 bivalents at meiosis, and are capable of limited reproduction by spores, this apomictic character being inherited from *D. affinis*. However, *D. x fraser-jenkinsii* shows no chromosome pairing at meiosis in 16-celled sporangia, whereas the new hybrid has 41 bivalents and 82 univalents at first metaphase in 16-celled sporangia (Fig. 1). Morphological comparison suggests that the new hybrid may be *D. affinis* subsp. *affinis* x *D. corleyi*, with which it grows. *D. corleyi* is a tetraploid species (Fig. 2) that may have originated from the diploid species *D. oreades* Fomin and *D. aemula* (Ait.) O. Ktze. (this is at present under investigation). Such a parentage could be compatible with the pairing seen in the hybrid, the bivalents being formed between the two 'oreades' genomes, one from *D. affinis* subsp. *affinis* and one from *D. corleyi*.

Dryopteris x asturiensis Fraser-Jenkins & Gibby hybr. nov.

(= *D. affinis* subsp. *affinis* x *D. corleyi*)

Planta hybrida morphologia intermedia inter parentes. Stipes et rhachis crassiores quam in *D. corleyi* paleis fulvis basibus valde densioribus vestitis. Frons deltato-lanceolata, pinnata; pinnae sessiles, infimae e pinnulis basalibus longis gradatim decrescentes; pinnulae infernae valde sed non profunde lobatae usque ad dimidium latitudinis inter costam et marginem, lobi lati rectangulares, superi non-lobati vel lobis minoribus rotundatioribus; apices pinnularum late rotundati vel in plantis minoribus rotundato-truncati, lobi et apices pinnularum aliquot crenas vel dentes non manifestos ferentes, velut saepe apicibus acutis. Indusia valde decurvata ad margines eorum, aliquid crassae et persistentia. Sporae abortivae, sed aliquot sporae magnae non-abortivae praesentiae.

Holotype: *Dryopteris x asturiensis* Fraser-Jenkins & Gibby. c. 100m, in wood on sandstone 2km below Puron, c. 7km SE of Llanes, Oviedo to Santander, Oviedo (Asturias), Spain. C.R. Fraser-Jenkins 10835, 5 Oct. 1981 (BM) Fig. 3.

Isotypes: Ditto (MA; Herb. T. Reichstein, Basel).

Paratypes: c. 50m, in wood on sandstone above main Oviedo to Santander road, above Pendueles village, c. 2km E of Vidiago, E of Llanes, Oviedo to Santander, Oviedo (Asturias), Spain. C.R. Fraser-Jenkins 10778 (BM! K! MA! P!), 10779 (BM!), 10780 (BM!), 10781 (BM!), 10798 (BM! Herb. M. Laínz, Gijón University!).

Plants occurring with both parents and also *D. dilatata*, *D. affinis* subsp. *borreri* (Newm.) Fraser-Jenkins and *D. filix-mas* (L.) Schott. Morphology intermediate

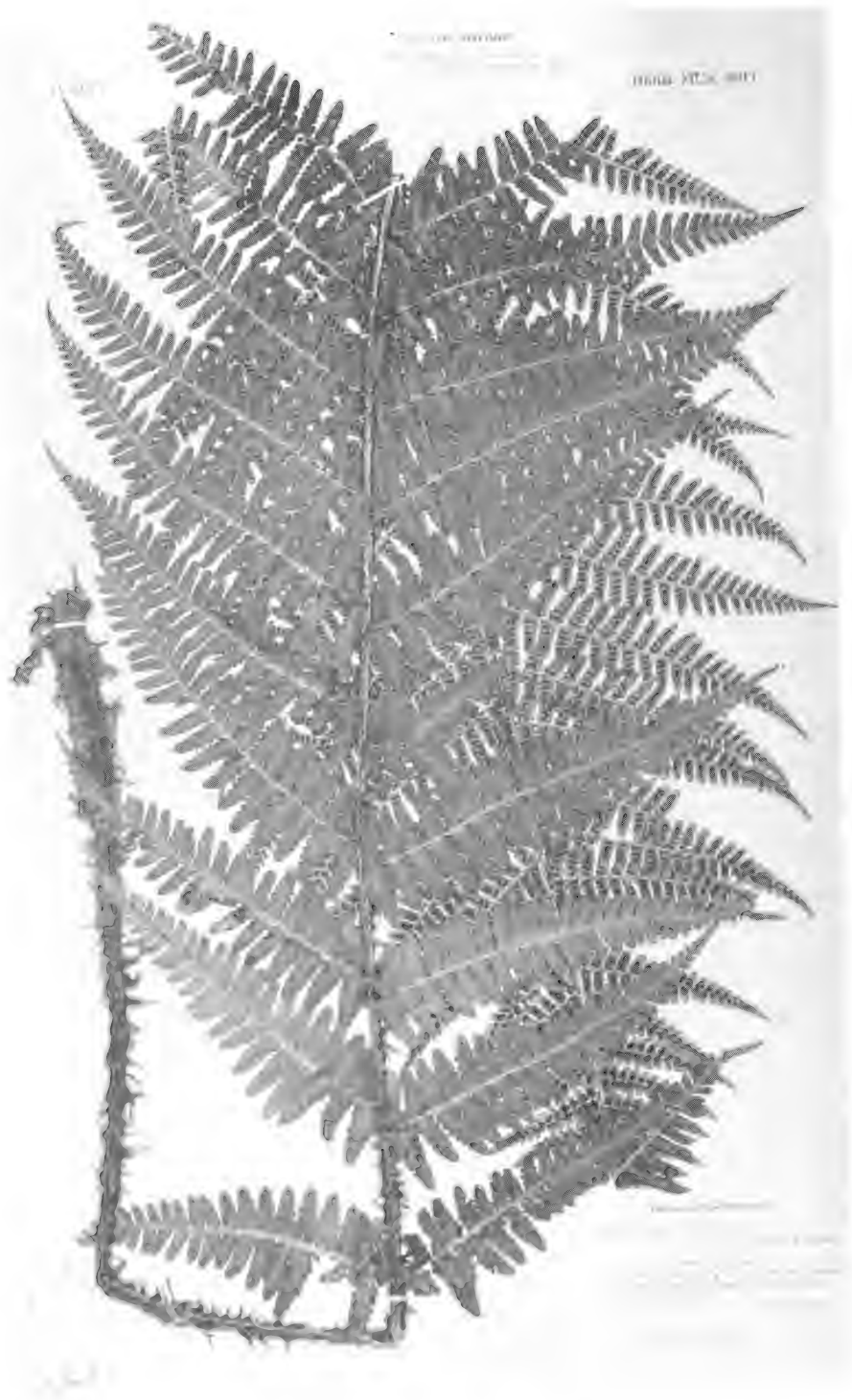


FIGURE 3 *Dryopteris x asturiensis* CRFJ 10835 holotype.

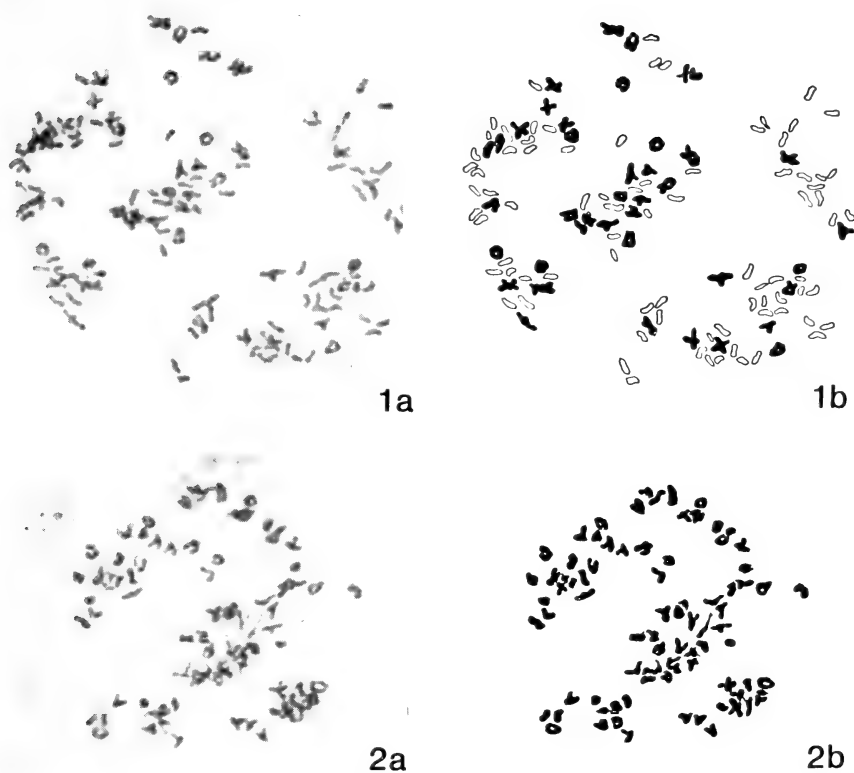


FIGURE 1a *Dryopteris x asturiensis* CRFJ 10835 spore mother cell from 16-celled sporangium at diakinesis showing 41 bivalents and 82 univalents; b explanatory diagram with bivalents in black, univalents outlined, x 750.

FIGURE 2a *Dryopteris corleyi* CRFJ 10782 spore mother cell at diakinesis showing 82 bivalents; b explanatory diagram, x 750.

between the parents. Stipe and rhachis thicker than in *D. corleyi* and markedly more densely clothed in light brown scales with dark bases. Frond deltate-lanceolate, once pinnate; pinnae sessile, the lowest ones gradually tapering from long basal pinnules; lower pinnules markedly but shallowly lobed up to half the width between the midrib and margin with wide, rectangular lobes, upper pinnules unlobed or with smaller, more rounded lobes; pinnule apices broadly rounded, or in smaller plants, rounded-truncate, the lobes and pinnule apices bearing a few insignificant crenations or obtuse teeth, though often with pointed apices. Indusia strongly curved down at their margins, somewhat thick and persistent. Spores abortive but with a few large, good spores present. Differs from *D. affinis* in its long stipe, deltate-lanceolate frond, long lowest opposite pair of pinnules on the lower few pairs of pinnae, much more deeply lobed pinnules, the lower ones with narrower apices, and mostly abortive spores. Differs from *D. corleyi* in its denser and browner scales, many with dark bases, its thicker stipe and rhachis, more sessile pinnae and pinnules, less lobed lobes or divided pinnules, markedly broader pinnule apices, thicker indusia and mostly abortive spores. Differs from *D. x fraser-jenkinsii* in its slightly paler stipe scales, markedly broader, less pointed pinnule apices, more rounded pinnule lobes with shorter, less acute teeth, and a generally flatter lamina with less twisted segments.

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- GIBBY, M. & WIDÉN, C.-J. 1983. Three new *Dryopteris* hybrids from Spain and the Canary Islands. *Fern Gaz.* 12: 267-270.

REVIEWS

MED-CHECKLIST 1 PTERIDOPHYTA (ed. 2) GYMNOSPERMAE DICOTYLEDONES (ACANTHACEAE-CNEORACEAE) edited by W. Greuter, H.M. Burdet & G. Long. 330+ C pp. 312 x 210mm. Published by Conservatoire et Jardin botaniques, Ville de Genève, Med-Checklist Trust of OPTIMA, Genève ISBN 2-8277-0151-0, ISBN 2-8279-0004-1, 1984.

This is a checklist of vascular plants from all the countries that border on the Mediterranean, plus Portugal, Bulgaria, the Crimea and Jordan. The taxonomic advisers for pteridophytes are C.R. Fraser-Jenkins, A.C. Jermy and T. Reichstein, and the book includes over 150 fern species. For each species the name, authority and source is given and synonyms, and the distribution (by country) within the Mediterranean region. For recent or doubtful records the reference is given in the appendix. Unfortunately some of the names used in this checklist are not those found in Hegi's *Illustrierte Flora von Mitteleuropa* (Kramer 1983; see review p.112) which was published in the same year, and this must reflect an editorial decision, since C.R. Fraser-Jenkins and T. Reichstein were pteridophyte advisers for Hegi. For example, the Med-Checklist uses *Lycopodium* for all the Lycopodiaceae, whereas Hegi uses *Lycopodiella*, *Diphasiastrum* etc., and such disagreement is frustrating for all pteridologists. However, the Med-Checklist, which uses a computerized system for information processing, formatting etc. and thus minimizing typographical errors, provides a valuable reference source.

M. GIBBY

EVOLUTIONARY CLADISTICS OF MARATTIALEAN FERNS by Christopher R. Hill & Josephine M. Camus. Bulletin of the British Museum (Natural History), Botany series Vol. 14 No. 4. 27 February 1986. Price £14.50.

The application of cladistic methods to problems of fern taxonomy has not, as yet, been widespread. It is encouraging, therefore, to read this paper on the classification of Marattiales which relies on cladistics to resolve relationships within the order. The concepts and terminology of the method are given, which is useful for those readers unfamiliar with cladistics. All species of the order have not been included, but the 23 species selected cover the range of variation in each of the extant genera; 73 characters are used ranging from the stelar anatomy of the adult stem to the shape of the exine spines of the spores. The resulting cladogram indicates the distinctness of both *Christensenia* and *Danaea*, and the paraphyletic nature of *Marattia*, *Macroglossum*, *Angiopteris* and *Archangiopteris*. As a check on the taxonomic relationships defined by the cladogram the authors have used stratigraphy, phytogeography and ontogeny, and present a convincing case for their conclusions. I look forward very much to seeing their further work on revising the genera and species of Marattiaceae.

B.S. PARRIS

SUBGENERIC NAMES IN *SELAGINELLA*

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ABSTRACT

In an account of Selaginellaceae to be published in *The Families and Genera of Plants: Pteridophyta* (ed. Kramer et al.) the author proposes five subgenera in the sole genus *Selaginella*: *Selaginella*, *Ericetorum* Jermy, *Tetragonostachys* Jermy, *Stachygynandrum* (P. Beauv.) Baker and *Heterostachys* Baker. In this brief synopsis the names *Ericetorum* Jermy and *Tetragonostachys* Jermy are described and validated.

INTRODUCTION

The genus *Selaginella* contains approximately 700 species for the most part concentrated in the tropical areas of the world. Botanists of the late eighteenth century (e.g. Adanson, Boehmer, Palisot de Beauvoir) describing the relatively small number of species available to them at that time saw generic distinctions that cannot be upheld today. Kuntze (1891), in the belief that *Lycopodioides* Boehmer was the earliest name for the genus, published some 320 new combinations in that genus. Rothmaler (1944) proposed acceptance of these earlier generic names but large-scale nomenclatural changes have not been published without the broad revision of the classification of the family that is needed. The present author, having studied *Selaginella* in some detail throughout its range, has proposed in a forthcoming book (*The Families and Genera of Plants: Pteridophyta*, ed. K.U. Kramer et al.) the following infrageneric classification which is published here in synopsis only in order to validate two of the names used. A full account of the morphology and relationships of these taxa is in preparation.

SELAGINELLA P. Beauv.

Palisot de Beauvoir, *Magasin Encycl.* 5: 478 (1804); *Prod. fam. Aetheog.* 101 (1805), em. Spring in *Flora* (Regensb.) 21: 148 (1838); nomen conserv.

Subgenus *Selaginella*. Type-species *Selaginella spinosa* P. Beauv. = *Selaginella selaginoides* (L.) Link.

Syn.: Subgen. *Homoeophyllum* (Spring) Hieron. & Sadeb. in Engler & Prantl, *Nat. Pflanz.* 1 (4): 669 (1902) p.p.

Stems erect, new primary shoots arising from the base upon maturation of the single terminal strobilus, rooting from a basal hypocotylar node; leaves and sporophylls spirally arranged, uniform and herbaceous.

Two species: *S. selaginoides* — circumboreal in the Northern Hemisphere, south to the Canary Islands; *S. deflexa* Brackenridge — endemic to Hawaiian Islands.

Subgenus *Ericetorum* Jermy subgen. nov.

Syn.: Subgen. *Homoeophyllum* (Spring) Hieron. & Sadeb. in Engler & Prantl, *Nat. Pflanz.* 1 (4): 669 (1902) p.p.

Rami erecti, aut ramosi aut rarius simplices, e caule repenti solenostelam continenti procumbente, exorientes; folia aequabilia, saltem ad basin decussata, plus minusve herbacea, lamina ovata vel ovato-lanceolata; sporophylla tetrasticha.

Type-species *Selaginella uliginosa* (Labill.) Spring, *Bull. Acad. R. Belg.* 10: 136 (1843). Stems erect, either unbranched or more compound, arising from a creeping solenostelic stem; leaves uniform, decussately arranged at least below, more or less herbaceous with an ovate or ovate-lanceolate lamina; sporophylls tetrastichous.

Three species: *S. uliginosa* — Australia and Tasmania; *S. gracillima* (Kunze) Spring — SE Australia; *S. pygmaea* (Kaulf.) Alston — southern Africa.

Subgenus *Tetragonostachys* Jermy **subgen. nov.**

Syn.: Subgen. *Homoeophyllum* (Spring) Hieron. & Sadeb. in Engler & Prantl, Nat. Pflanz. 1 (4): 669 (1902) p.p.

Planta repens, caulibus pleuriramosis, per totam longitudinem radices emittentibus, prostrata et saepe tegetes formans, vel humilis ramis erectis; folia spiraliter disposita, aequabilia vel in ramis prostratis dimorphescentia, plerumque coriacea, lineari-lanceolata, apice aliquando acicularia vel apice pilum praedita; sporophylla tetrasticha. Type-species *Selaginella rupestris* (L.) Spring, Flora 21: 149 and 182 (1838).

Plants creeping, stems much-branched, rooting throughout their length, prostrate and often mat-forming or with short erect branches; leaves spirally arranged, similar, or on prostrate branches slightly dimorphic, usually coriaceous, linear-lanceolate, apex sharp or bearing a hair; sporophylls tetrastichous.

About 50 species ranging from southern North America through the tropics of South America, Africa and the Indian subcontinent to N China and Japan.

Subgenus *Stachygynandrum* (P. Beauv.) Baker, J. Bot., Lond. 21:3 (1883) emend. Jermy, Fern Gaz. 13:118 (1986). Basionym: *Stachygynandrum* P. Beauv. ex Mirbel in Lam. & Mirbel, Hist. Nat. Veg. 3: 477 (1802). Type-species *Lycopodium flabellatum* L. = *Selaginella flabellata* (L.) Spring.

Syn.: Subgen. *Heterophyllum* Hieron. & Sadeb. in Engler & Prantl, Nat. Pflanz. 1 (4): 673 (1902); subgen. *Homostachys* Baker, J. Bot., Lond. 21: 4 (1883).

Stems either creeping with prostrate branches, or erect with various and often complex branching systems, leaves dimorphic, at least on the secondary branches, in four distinct rows, those of the upper rows being distinctly smaller; sporophylls uniform, or in a few cases showing slight dimorphism, tetrastichous.

Baker's concept is enlarged to include those species (*S. ciliaris* (Retz.) Spring; *S. pallidissima* Spring) he separated as being in his fourth subgen., *Homostachys*. Those species and others, such as those included in that subgenus by Walton & Alston (1938), have loose strobili with sporophylls that begin to show some dimorphism. In my opinion, and in that of N. Quansah (pers. comm.) who has studied the African species in detail these can rightly be included in subgen. *Stachygynandrum*.

About 600 species ranging throughout the tropics of all continents.

Subgenus *Heterostachys* Baker, J. Bot., Lond. 21: 4 (1883). Lectotype-species *Selaginella heterostachys* Baker, J. Bot., Lond. 23:177 (1885).

Syn. subgen. *Heterophyllum* Hieron. & Sadeb. in Engler & Prantl, Nat. Pflanz. 1 (4): 673 (1902).

Stems creeping and much-branched, or secondary branches erect and suffrutescent, rooting in branch axils; leaves as in subgen. *Stachygynandrum*; strobili complanate, sporophylls dimorphic, tetrastichous, those on the ventral side smaller than those on the upper side of the shoot.

About 60 species with a distribution range similar to that of subgen. *Stachygynandrum*.

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SHORT NOTES

THE OCCURRENCE OF *SCHIZAEA DICHOTOMA* IN TANZANIA

The curious and primitive fern *Schizaea dichotoma* (L.) Smith has been discovered recently in the Uzungwa mountains of Tanzania in the Mwanihana Forest Reserve above Sanje village at latitude 7°50'S and longitude 36°55'E. It is now known from three collections, which represent the first records of the species in continental Africa. Its previous known range was Madagascar to Polynesia and Australia (Holtum, 1968), where it is widespread and frequently collected.

In Tanzania it grows on the forest floor in leaf litter under a canopy of *Albizia gummifera*, *Filicum decipiens*, *Funtumia africana*, and *Parinari excelsa*, with the saprophytic herb *Seychellaria africana*, at an altitude of between 900-1200m. The forests themselves occur on the east facing slopes of the ancient crystalline Uzungwa mountains in an annual rainfall of 2000-2500mm, and are well known for the high degree of endemism they contain (Lovett, in press).

In view of the previous known range of *Schizaea dichotoma*, the question arises as to whether its distribution pattern is a relict which predates the break up of Gondwanaland and the separation of Madagascar from continental Africa, or whether its occurrence in Tanzania is a result of later long distance dispersal from Madagascar. The former idea has been suggested to explain the distribution of the bryophyte family Rutenbergiaceae which also occurs on the ancient crystalline East African mountains and Madagascar (Pocs, 1975). However, for *Schizaea dichotoma*, long distance dispersal is perhaps more likely in view of its limited distribution in Tanzania, and its spores might be carried by the prevailing winds from Madagascar to Tanzania.

Interestingly enough the associate of *Schizaea dichotoma*, *Seychellaria africana*, which is currently only known from the Uzungwa mountains, belongs to a genus which is otherwise only found on Madagascar and adjacent islands (Vollesen, 1980). Perhaps it too reached Tanzania by long distance dispersal of its small seeds. The association of *Schizaea* and *Seychellaria* is even more curious in that it has been noted in the Neotropics that *Schizaea* is found in association with saprophytic plants in the same family as *Seychellaria*, the Triuridaceae (Maas, 1979), and the fact that this condition is also found in Tanzania may suggest that *Schizaea* is also saprophytic to some degree.

I am grateful for the assistance of Barbara Parris in the identification of Tanzanian ferns, and the Tanzania National Scientific Research Council who very kindly gave me permission to conduct field work in Tanzania. The National Geographic Society and World Wildlife Fund generously provided the support for the field work.

Collection numbers from the Tanzanian locality are: Lovett 244, (K, DSM) Stuart & Rodgers 838 (K, DSM), Thomas 3699 (K, MO).

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A CHROMOSOME COUNT FOR *ANOGRAMMA LEPTOPHYLLA* IN MADEIRA

A comprehensive study of the cytology of the native ferns of Madeira has recently been completed (Manton et al. 1986). However, for one fern, *Anogramma leptophylla* (L.) Link, a definitive count proved difficult, owing in part to a tendency for clumping of the chromosomes but also to the annual habit of the fern. In early Spring of this year J.F.M. and M.J. Cannon made fixings in the wild (Madeira: Levada from Boco do Risco east to Canical tunnel entrance. Cannon & Cannon 5169, 10 March 1986. BM), and a chromosome count of 26 bivalents at meiosis has now been confirmed (Fig. 1). This is in agreement with Fabbri (1963) quoting Tutin as 'n = 26?' for material from Jersey, and Kurita (1971) who gives n = 26 for material from Europe without giving a precise locality, and contrasts with counts of n = 29 for this species from New Zealand (Brownlie 1958) and South Africa (Baroutsis & Gastony 1978), and n=56-7 (Mehra & Verma 1960) and n=58 (Verma, quoted by Manton et al. 1986) from India.

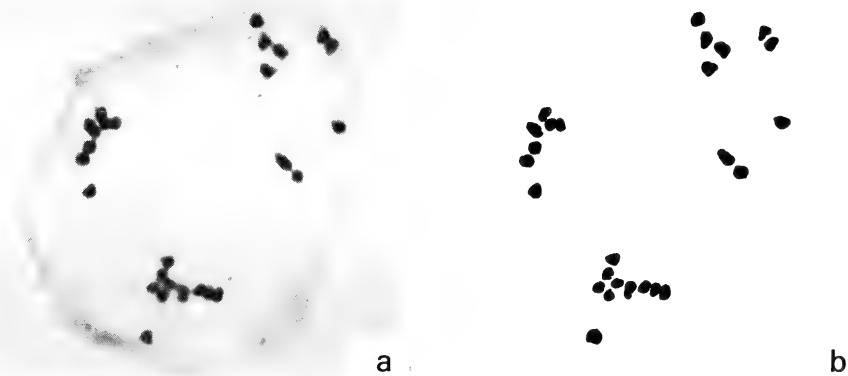


FIGURE 1a Spore mother cell of *Anogramma leptophylla* at metaphase 1 showing 26 bivalents; b explanatory diagram, x 1000.

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CYSTOPTERIS IN THE CAPE VERDE AND CANARY ISLANDS

The specimens of *Cystopteris* which I collected in the Cape Verde Islands have been published by me as *C. fragilis* sens. lat. (Lobin, 1982).

Now, using the vein character of Rocha Afonsa (1982) and the spore characters I myself have observed, I can say that the Fogo (Cape Verde Islands) specimens are *C. fragilis* (L.) Bernh. and that the specimens which I collected on Tenerife (Canary Islands) are *C. viridula* (Desv.) Desv. The key characters I used are:

Veins ending in the apex of the teeth; spores echinate, loosely covered with spines \pm equal in size and shape *C. fragilis*

Veins ending in the sinus between two teeth; spores spiny-lacunar, so densely covered with spines unequal in size and shape and connected at their base, that they obscure the surface *C. viridula*

C. fragilis was discovered in the Cape Verde Islands in 1863 by A. Stübel (Bolle, 1866). A second collection of this rare fern was made by Chevalier (1935) and the third by Barbosa (Nogueira, 1975). I found the species growing at Fogo in the walls of small shady humid valleys (ribeiras) at about 800 to 1200m alt. and apart from one specimen in the southwest, all on the north side.

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CYSTOPTERIS VIRIDULA IN MAINLAND AFRICA

Although known from the Cape Verdes, Macaronesia, south-west Europe, west Mediterranean Europe, Morocco and Algeria, *Cystopteris viridula* (Desv.) Desv. has not so far been reported from mainland Africa (in the floristic sense). My father and I recently found it on Mount Oku in North-West Province, Cameroon: above road on NE side of Mt. Oku, c. 4km SE of Oku on Kumbo road, NE of Bamenda, c. 2300m alt., on moss-covered boulder in dense natural forest by stream, above encroaching potato fields. Coll: CDFJ & CRFJ 11489, 6 June 1985 (BM, H).

This suggests that this species could be yet another example of the African affinity of much of the Macronesian and Atlantic European floristic element in ferns, which I see as secondarily invading south-western Europe in many cases, though often with presumed more ancient Asian connections, sometimes via Africa. I have not yet been able to investigate other west or central African populations of the *Cystopteris fragilis* (L.) Bernh. group from the Tibesti, Hoggar etc.

ACKNOWLEDGEMENTS

The author would like to thank his father, C.D. Fraser Jenkins of Bridgend, the Botanical Museum, University of Helsinki and Professor T. Reichstein for their generous financial help.

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FIRST RECORD OF *EQUISETUM* *x* *DYCEI* IN CONTINENTAL EUROPE

During a botanical survey of plants growing in the "Maximilianpark" in the vicinity of Hamm (North Rhine-Westphalia, Federal Republic of Germany) one of us (U.P.) collected a strange looking horsetail which at first was thought to represent *Equisetum x litorale* Kühlew. ex Rupr. Further studies revealed, however, that the plants showed closer relationships to *E. palustre* L. than to *E. arvense* L. Our tentative determination as *E. x dycei* C.N. Page was subsequently confirmed by C.N. Page to whom we sent our plants for examination. As far as we know this is the first record of *E. x dycei* outside the British Isles and the first for continental Europe. Diagnostic features of this hybrid are given by Page (1982).

The environmental conditions of the *E. x dycei* stand in Hamm are similar to those described by Page (1985) for the British and Irish localities. It is a wet habitat being permanently flooded by shallow water and has been disturbed or at least modified in some degree by man. This occurred recently during the development of the whole area for the "Landesgartenschau", an open air display of ornamental flowers exhibiting modern trends and features of garden architecture, which took place in 1984. In the course of the work the site where *E. x dycei* grows was covered with loamy soil and an artificial water regime installed to keep the site flooded. Additionally, several species of macrophytes (e.g. *Lythrum salicaria*, *Typha angustifolia*, *Carex acutiformis*) were planted to re-create a vegetation cover. Both parental species of *E. x dycei*, *E. palustre* and *E. fluviatile* L., are present, but only a small number of shoots; these have not been planted. The vegetation is still very scarce and open, and this is another common feature with the Scottish and Irish localities. Here the rather few (about 20), small and weakly growing shoots of *E. x dycei* persist. This hybrid appears to be a weak competitor and disappears as soon as other plants start to grow more vigorously and vegetation becomes more dense. This is very much in contrast to *E. x litorale* which can form large colonies and seems to compete quite successfully with many other plant species. The whole circumstances suggest that the *E. x dycei* stand in Hamm originated there only a few years ago.

Although it is difficult to make any predictions on the future development of the population we are inclined to believe that the plants will not survive for a very long time. The stand could be adversely affected by both enhanced growth of other macrophytes and possible disturbance of the habitat by recreational activities.

Regarding the distribution of *E. x dycei* we fully agree with the statement of Page (1985) that *E. x dycei* can very easily be overlooked and it may well turn out that it is more frequent on the European continent than this one reported locality suggests.

ACKNOWLEDGEMENTS

We thank Dr C.N. Page, Edinburgh, for his kind support and for examining our *Equisetum* specimens and Mr Ralph David, Witten, for improving our English.

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AN ANOMALY OF *BOTRYCHIUM MATRICARIIFOLIUM*

In August 1985 the author found one specimen of *Botrychium matricariifolium* A.Br. ex Koch in the hills of the Českomoravská Vrchovina about 70km northwest of Brno (Czechoslovakia). It was surprising to see that it bore sporangia on the sterile part of its frond.

Since this specimen was rather old when it was found it was impossible to determine the correct species at once so it was sent to Prof. Dr. Follmann (Köln) for detailed analysis. He ascertained the abnormal sporangia to be stunted and the number of chromosomes to be about 180. As *B. virginianum* (L.) Sw. must be eliminated because of its very different habit the specimen can only be *B. matricariifolium*.

For further details the author may be contacted. Special thanks are due to Prof. Dr. Follmann for his efforts.

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CORRECTIONS TO INDEX FILICUM

Index filicum is now produced by the Royal Botanic Gardens, Kew, and as the new editor I am keen to correct the errors in the original and subsequent supplements. I am aware of a number of these but am sure that others are as yet undetected. I very much welcome information on any omissions and mistakes known to my colleagues. Intraspecific names are to be included in the next supplement, which will run from 1976-1985. From 1986, new names of pteridophytes will be published annually, as an appendix of an annual *Index Kewensis*, but *Index Filicum* will continue to be published at 5 or 10 year intervals.

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OBITUARY

PROFESSOR E.A.C.L.E. SCHELPE

Professor Edmund André Charles Lois Eloi ('Ted') Schelpe died after a sudden heart attack at his home on Saturday 12th October 1985. Professor Schelpe was born in Durban on 27th July 1924. He completed a BSc with distinction in Botany at Natal University in 1943 and at the same University obtained an MSc (Class I) in 1946. He obtained the DPhil degree of Oxford University (Wadham College) in 1952. He held the following posts at the University of Cape Town: Lecturer in Botany, 1953-1954; Senior Lecturer and Curator of the Bolus Herbarium, 1954-1958; Associate Professor and Curator of the Bolus Herbarium, 1968-1973, the title Curator being changed to Director from 1970; Professor (ad hominem) and Director of the Bolus Herbarium, 1973-1985. Professor Schelpe was an elected Fellow of the Royal Society of South Africa, the Linnean Society of London, and the University of Cape Town. From 1964 he had been a Member of the Committee on Pteridophyta of the International Association of Plant Taxonomists. Professor Schelpe has made major contributions to the systematics of Pteridophyta in southern Africa. A few days before he passed away he finished checking the final proofs of the Pteridophyta volume for the *Flora of Southern Africa*. This was a culmination of studies in the course of which he published the accounts of the Pteridophyta for the *Flora Zambesiaca*, the *Flora de Moçambique* and the *Conspectus Florae Angolensis*. He published over 100 scientific papers and books, which besides Pteridophyta covered topics in orchids, bryophytes, plant ecology and phytogeography. Professor Schelpe was a distinguished and internationally well-known botanist and his passing away is a sad loss to the scientific community.

Information supplied by A.V. HALL
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REVIEWS

FERNS OF JAMAICA by G.R. Proctor. 631 pp., 135 figures, 22 maps, 175 x 250mm. British Museum (Natural History), London. ISBN: 0-565-00895-1. 1985. Price £50.00.

Jamaica is an island especially rich in ferns for which no adequate modern handbook was available. The defect has now been remedied in a very authoritative manner by the publication of this book. All groups of pteridophytes are covered and some idea of the richness of the flora and the technical problems facing the author can be gained from the fact that 579 species and a further 30 clear varieties are described.

A very valuable feature of the short Introduction is the listing of the 178 collectors known to have gathered ferns in Jamaica, together with their collecting dates and herbaria where the author has seen their specimens.

The main text is easy to read and well laid-out — thus for each family there is a general account and a note on any special literature, followed by clear keys to the genera. The species entries are concise and informative, giving the detailed authority, the type specimen, basionym and synonyms, species description, general range and Jamaican distribution and a short entry on habitat, together with comment as to relative abundance in Jamaica.

The specific descriptions average some 10-12 lines and are clear proof of Dr Proctor's familiarity with the plants in the field. Use has been made of published cytological evidence where this has thrown light on a particular taxonomic aspect such as the separation of taxa and the recognition of hybrids, etc.

In taking a wide view of such genera as *Thelypteris*, *Polypodium*, *Grammitis*, *Cyathea*, etc., and by maintaining a hierarchy based on the subgenus, Proctor is of the opinion that the ends of classification are thus best served. All the keys are clear and well-constructed and avoid the use of comparative terms which are an unfortunate feature of some works and are of little use unless the student has both taxa to examine. The acid test of any key is how easy and accurate it is in use and I selected eight of the largest genera and from these pulled out at random folders of 20 species, all of which keyed out satisfactorily. There was one discrepancy, namely in the key leading to *Polypodium loriceum* where the rhizome was said to be "bearing a few scattered appressed scales, otherwise naked" whilst the specific description (p.529) describes the rhizome as bearing numerous appressed scales. Indeed, in the same folder of *P. loriceum* that I examined, some specimens had numerous rhizome scales whilst others had very few. Nevertheless despite this difficulty the keying process still gave the right answer because of the other alternatives.

A delightful feature of the book is in the illustrations. Seventy five of the 83 native genera are delineated and a very skilful choice has been made to demonstrate a range of artistic styles and printing methods — some old such as those from Rovirosa, Hooker, Schkuhr, etc., and others modern from Small, Stolze and A.R. Smith for example. In a number of cases excellent original drawings by P.J. Edwards are included.

In summary, this is an invaluable work written by the leading authority on Jamaican ferns who has built up an intimate knowledge of these plants in the field over many years and who has put this to use in a very clear and concise manner. No one who has an interest in these ferns can afford to be without this book, although the price is somewhat daunting. I hope that we may look forward to sequels covering the history of plant collecting in Jamaica and an account of the ecology and behaviour of these ferns.

It may be somewhat churlish to adversely comment on a feature of such an excellent book, especially as it is not the responsibility of the author, but mention must be made of the binding. Books of this type which are going to be used extensively both in the laboratory and the field will be subject to quite heavy wear and tear. A first essential is to provide covers which will stand up to this and which preferably should be waterproof or wipeable. In the short time I have had my copy (which has only been used in the laboratory) the cover is showing dirty marks and on attempting to wipe them off the red dye has come away. In addition the corners are fraying. Surely more thought could be put by publishers to the use to which a book is going to be put and provide more appropriate covers, particularly in view of the high price of books in general.

T.G. WALKER

GAMETOPHYTES OF OPHIOGLOSSACEAE by D.D. Pant, D.D. Nautiyal and D.R. Misra. *Phyta Monograph 1: 1-111*. 1984. 180 x 250mm. Published by the Society of Indian Plant Taxonomists, Allahabad, 211002. India. Price not given.

This is a thorough descriptive account of the gametophytes of six species of *Ophioglossum*, four of *Botrychium* and *Helminthostachys zeylanica*, and an historical review of work on the subject. The gametophytes of Ophioglossaceae are geophilous, cylindrical, fleshy and tuberous, and for the most part monoecious. Xylem stands are shown to be present in the centre of the prothallus of *H. zeylanicum* and comparisons are suggested with the fossil *Rhynia gwynnevaughanii*, thought by some to be a highly organised prothallus. The book is well illustrated both with photomicrographs and well executed line drawings.

A.C. JERMY

BRITISH PTERIDOPHYTE RECORDS

Compiled by A.J. Worland

Since the appearance of the 'Atlas of Ferns', an annual list of additions and corrections has been compiled from information supplied by the Biological Records Centre, BSBI vice-county recorders and members of the BPS and BSBI. Lists have been published in the BPS 'Bulletin' up to and including 1982 and subsequently annually in the *Fern Gazette*.

The records are presented thus: 100km square (letters are used for Irish grid squares to avoid confusion)/10km square followed by the recorder's name. Nomenclature follows the Atlas. The following additions have been received up to the end of March 1986.

POST 1980

- 2.1 *Lycopodiella inundata* E Cumberland, R.W.M. Corner
- 5.2 *Selaginella kraussiana* 36/67 E.P. Beattie
- 7.1 *Equisetum hyemale* 37/41 N.F. Stewart
- 7.1x2 *E. x trachyodon* 35/37 G. Halliday, 35/78 G.A. Swan
- 7.2 *E. variegatum* H12/37 F. Bonham
- 7.3 *E. fluviatile* 53/04 N.J. Hards
- 8.1 *Botrychium lunaria* 25/67 V. McClive
- 14.1 *Hymenophyllum tunbrigense* 26/25 B. Simpson
- 16.1 *Polypodium vulgare* 52/94 E.M. Hyde, 62/13 E.M. Hyde
- 16.2 *P. interjectum* 53/05 N.J. Hards
- 16.2x1 *P. x mantoniae* 52/94, 62/03, 62/13 E.M. Hyde
- 17.1 *Pteridium aquilinum* 53/24 N.J. Hards
- 18.1 *Thelypteris thelypteroides* 22/93 R.G. Woods, H12/27 F. Bonham
- 20.1 *Oreopteris limbosperma* 34/86 N.J. Hards, 51/04 M.D. Reed
- 21.1 *Asplenium scolopendrium* 53/04 N.J. Hards
- 21.2 *A. adiantum-nigrum* 43/97, 53/04, 53/14 N.J. Hards
- 21.6 *A. marinum* 36/68 M. McAffer
- 21.7a *A. trichomanes* subsp. *trichomanes* 22/72 R.N. Stringer & I.K. Morgan
- 21.11 *A. ceterach* 26/40 B. Simpson
- 22.1 *Athyrium filix-femina* 48/02 A.O. Chater, 53/34 N.J. Hards
- 26.2x3 *Polystichum x bicknellii* 18/52 M. Barron, 22/40 I.K. Morgan
- 26.3 *P. setiferum* 43/97, 53/34 N.J. Hards
- 27.2 *Dryopteris filix-mas* 53/24 N.J. Hards
- 27.3 *D. affinis* subsp. *affinis* 22/40 I.K. Morgan
- 27.3 *D. affinis* subsp. *borreri* 22/40 I.K. Morgan
- 27.3 *D. affinis* subsp. *stillupensis* 22/72 I.K. Morgan
- 27.5 *D. aemula* 41/22 F. Rose & R.J. Hornby
- 27.6 *D. villarii* subsp. *submontana* 35/90 R.G. Jefferson
- 27.8 *D. carthusiana* 34/85 N.J. Hards
- 27.9x8 *D. deweveri* 22/63 I.K. Morgan, 34/85 N.J. Hards
- 30.1 *Azolla filiculoides* 33/10 C.J. Harris, 33/20 M. Wainwright & E.D. Pugh,
44/63 E. Chicken

THE FERN GAZETTE

Original papers, articles or notes of any length on any aspect of pteridology will be considered for publication.

Contributions should be sent to:

Dr. M. Gibby, British Museum (Natural History), Cromwell Road, London SW7 5BD.

The *last* date for receiving notes and articles to make the following summer number is:

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Manuscripts: Copy should be in English and submitted in double-spaced type with adequate margins, on one side of the paper only.

Abstract: All papers, other than short notes, should include a short abstract, to be set at the head of the main text, indicating the scope of the topic and the main conclusions.

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Latin names: Quote the authority at (usually) the first mention only, in the main text but, unless unavoidable for clarity not in the title. All latin names should be underlined throughout the typed copy.

Illustrations: Any number and combination of line and half-tone illustrations (original drawings or diagrams in ink, or photographs **which must be black and white**, and of good technical quality) can be included with a manuscript where these help to augment or amplify the text. Photographs should be of the required magnification or larger and need not be made up to full page plates. Each drawing or photograph should be marked on the back with details of author and figure number, and the top edge clearly marked "top". Illustrations will not be returned to the author unless specifically requested.

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THE FERN GAZETTE

VOLUME 13 PART 2

1986

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THE FERN GAZETTE

Edited by

*J.A.Crabbe, M.Gibby
& B.S.Parris*

THE
BRITISH
PTERIDOLOGICAL
SOCIETY

Volume 13 Part 3

1987

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This number is dedicated to
PROFESSOR DOCTOR TADEUS REICHSTEIN,
eminent pteridologist,
on the occasion of his Ninetieth Birthday
20th July 1987

Photograph courtesy of H. & K. Rasbach

Further papers submitted to honour Professor Reichstein
will appear in the next number of the Fern Gazette

T. REICHSTEIN : A PERSONAL APPRAISAL

There can be no doubt that, in Tadeus Reichstein, now entering his 90th year, we have among us one of the most outstanding personalities of the 20th century. I am not erudite enough to discuss his chemical achievement *per se* except to note that in 1968 he was awarded the highest accolade in the gift of the Royal Society of London (the Copley Medal). Other aspects of his life and scientific interests can perhaps best be introduced in an anecdotal manner based on my own personal experience of how I first became involved with him.

This happened early in the 1950s when he wrote to me from the Chemistry Department in Basel to follow up some information that I had recently published in my book (Problems of Cytology and Evolution in the Pteridophyta, 1950, CUP). This book had been drawn to his attention by a Swiss colleague and he wanted to know how best to confirm the putative hybrid nature of some of his local ferns. In reply, I offered to visit him to look at them provided only that he could lay on any kind of a student's microscope. He replied by telegram saying "Splendid. Come this weekend". This message reached me at 12 noon on Whit Saturday and if one can effectively think back to that time there will be no doubt regarding the impossibility of flying to Switzerland at Whitsun if you don't know that you want to go before noon on Whit Saturday. I had to explain this also by telegram but having secured a flight as soon as possible at a later weekend (in term time I could not easily be absent from Leeds except at a weekend) I took the precaution, before setting off, of consulting our then professor of organic chemistry for information about my unknown correspondent. The reply I received was surprising, and at first alarming. I was told "Oh, Reichstein. He is a very well known mountain climber with many difficult traverses named after him". This rather frightening prospect was toned down by one additional fact, namely that he was now old and therefore might not want to dangle me on a rope over a precipice. Somewhat comforted by that I set off and was received with the most incredible hospitality and kindness. I had no difficulty in sorting out his problematical hybrids by showing him how to recognise bad spores under a microscope. I also took the opportunity of taking fixings of several plants that he had growing in his greenhouse from local gatherings and some of these, when looked at chromosomally after my return to Leeds proved to be new — diploids where tetraploids were to be expected or the converse. Herewith began an active collaboration that has lasted until the present day.

Even at the first encounter I was so much impressed with his ready intelligence as well his botanical expertise that I made more enquiries as soon as I got back to Leeds, this time from a student in the Chemistry Department. This lad's eyes opened wide as soon as I mentioned the name Reichstein. I was assured that he was a tremendous chemist and indeed the holder of a Nobel Prize (awarded in 1950). What a difference from the previous concentration on mountain climbing as a major credential, true as this doubtless is!

To a professional chemist, the very simple reagents needed (acetic acid and absolute alcohol) to take fixations for aceto-carmine squash preparations offer no problems and I was soon receiving new fixations of additional Swiss specimens. At first I dealt with these myself but soon began to pass them on to John Lovis (a member of my staff) who benefitted greatly by the experience. Since Reichstein himself owned a powerful car and was willing to apply his alpine expertise in any part of Europe (France, Spain, Germany, Italy etc.) as required, knowledge of European ferns rapidly increased. Certain key genera, notably *Asplenium*, *Polypodium*, *Dryopteris* etc., are now as fully known as they are likely to become, at least with respect to this part of the world. For this alone, I was able, in 1974, to propose Reichstein as an honorary foreign member of the Linnean Society of London, when I became president (1974-76) of that well known biological society.

Reichstein has now been able to stimulate his own local group to become experts both in cytology and in taxonomy thereby virtually eliminating any former dependence on Britain. Moreover, the Swiss group has recently turned the tables on Britain by giving invaluable help towards finalising a long drawn out project on the fern flora of Madeira begun by the Leeds group in 1949 but published only in 1986 (see *Bull. Brit. Mus. (Nat. Hist.) Bot.* 15: 123-161). By that time four authors had necessarily become involved namely I. Manton (Leeds), John Lovis (now permanently resident in New Zealand), G. Vida (Budapest) and Mary Gibby (London). Such a geographical spread among authors posed a major obstacle to communication and the text took two years to complete. Indeed, without Reichstein's constant help in co-ordinating nomenclature and literature and in detecting errors sometimes involving the typescripts of one or other author finality might never have been reached.

A pioneer as effective as this in so many different fields of human activity is rare indeed and anyone privileged to have known him personally can scarcely fail to be both proud and grateful for the experience.

Irene Manton

**ASPLENIUM X REICHSTEINII (= ASPLENIUM FONTANUM X
A. MAJORICUM; ASPLENIACEAE: PTERIDOPHYTA),
A NEW ENDEMIC FERN HYBRID FROM MALLORCA,
BALEARIC ISLANDS**

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ABSTRACT

An *Asplenium* hybrid that was found near the town of Sóller, Mallorca, is described and the name *Asplenium x reichsteinii* Bennert & Rasbach is proposed for it. It is a triploid plant exhibiting 36 bivalents and 36 univalents at meiosis. These cytological results as well as its morphology strongly suggest that it originated from a cross between *Asplenium fontanum* and *A. majoricum*. Further support in favour of this interpretation was obtained by comparing it with hybrid plants of this combination artificially produced by Sleep (1967); an almost complete agreement in morphology and an identical cytological pattern were both observed. The occurrence of *Asplenium fontanum* on Mallorca and earlier reports in literature of a single plant obviously also representing *Asplenium x reichsteinii* are discussed.

INTRODUCTION

Asplenium majoricum Litard. is an endemic fern of the Island of Mallorca where it occurs at only a few scattered localities, most of them in the close vicinity of Sóller (Jaquotot & Orell 1968). It is an allotetraploid species (Jermy & Lovis 1964) having originated from a cross between diploid *Asplenium petrarchae* subsp. *bivalens* (D.E. Meyer) Lovis & Reichstein and another diploid, *Asplenium fontanum* (L.) Bernh., by chromosome doubling (Sleep 1967, 1983; Lovis & Reichstein 1969; Lovis et al. 1969). Lovis (1977; p.326) succeeded in resynthesizing *Asplenium majoricum* from its diploid parents.

Obviously *Asplenium majoricum* hybridizes with other species of Aspleniaceae rather easily. Three described and named hybrids involving *Asplenium majoricum* are presently known, all of them found near Sóller: *Asplenium majoricum* x *A. trichomanes* subsp. *quadrivalens* D.E. Meyer (= *Asplenium x orellii* Lovis & Reichstein, Lovis & Reichstein 1969), *Asplenium majoricum* x *A. petrarchae* (Guérin) DC. subsp. *petrarchae* (= *Asplenium x sollerense*, Lovis, Sleep & Reichstein, Lovis et al. 1969), and finally the intergeneric hybrid *Asplenium majoricum* x *Ceterach officinarum* DC (= *x Asplenoceterach barrancense* Bennert & D.E. Meyer, Bennert & Meyer 1972).

During an excursion to the olive groves above Biniaraix near Sóller, Mallorca, in April 1986 two plants were found that were believed to represent the cross between *Asplenium fontanum* and *A. majoricum*. The area was revisited in October 1986 and another four hybrid plants were discovered. Results of further studies, especially the cytological examinations, confirmed the assumed origin of this hybrid. It is described here in detail and named *Asplenium x reichsteinii*.

MATERIALS AND METHODS

The two plants of *Asplenium x reichsteinii* found in April 1986 were collected and taken into cultivation in the greenhouse of Prof. Reichstein at Basel and at Bochum for further studies. In October 1986 another plant (out of a group of three plants growing closely together) was taken into cultivation at Basel. Of the fourth plant found in

October 1986 fixations were made in the field. The meiosis was investigated applying the classical acetocarmine method (Manton 1950). For the final analysis and the photographs of the spore mother cells a magnification of 1,000 x and a phase microscope were used. In the case of the type plant 18 cells in the stage of diakinesis/metaphase 1 were counted.

DIAGNOSIS

***Asplenium x reichsteinii* Bennert et Rasbach *hybr. nov.* (= *Asplenium fontanum* (L.) Bernh. x *Asplenium majoricum* Litard.).**

Planta hybrida, media inter parentes, sed *Asplenio fontano* aliquid similior. Ab hoc distinguitur: pinnae magis compactae, minus profunde incisae. Sporae abortivae. Planta triploidea, meiosi chromosomatibus bivalentibus 36, univalentibus item 36.

Holotype: *Asplenium x reichsteinii* Bennert et Rasbach. On a limestone wall above Biniaraix near Sóller, Mallorca, Balearic Islands, Spain; c. 180m alt.; with *Asplenium majoricum*, *A. petrarchae*, *A. trichomanes*, and *Ceterach officinarum* growing in the near vicinity; leg.: H.W. Bennert et U. Peters, 17 April 1986; WB SP 43/86; plant later cultivated in Basel under reference number TR-6477; whole plant pressed on 7 October 1986; holotype: **B** (see Fig. 1).

Dedicated to Prof. Dr. T. Reichstein, Basel, who has added very much to the knowledge of the ferns, especially of the genus *Asplenium*.

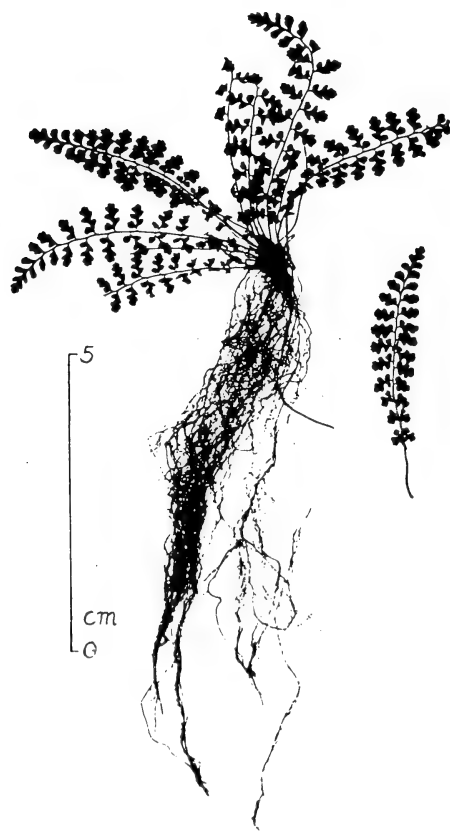


FIGURE 1. *Asplenium x reichsteinii* Bennert et Rasbach (= *Asplenium fontanum* x *A. majoricum*); silhouette of the type plant (kept in B).

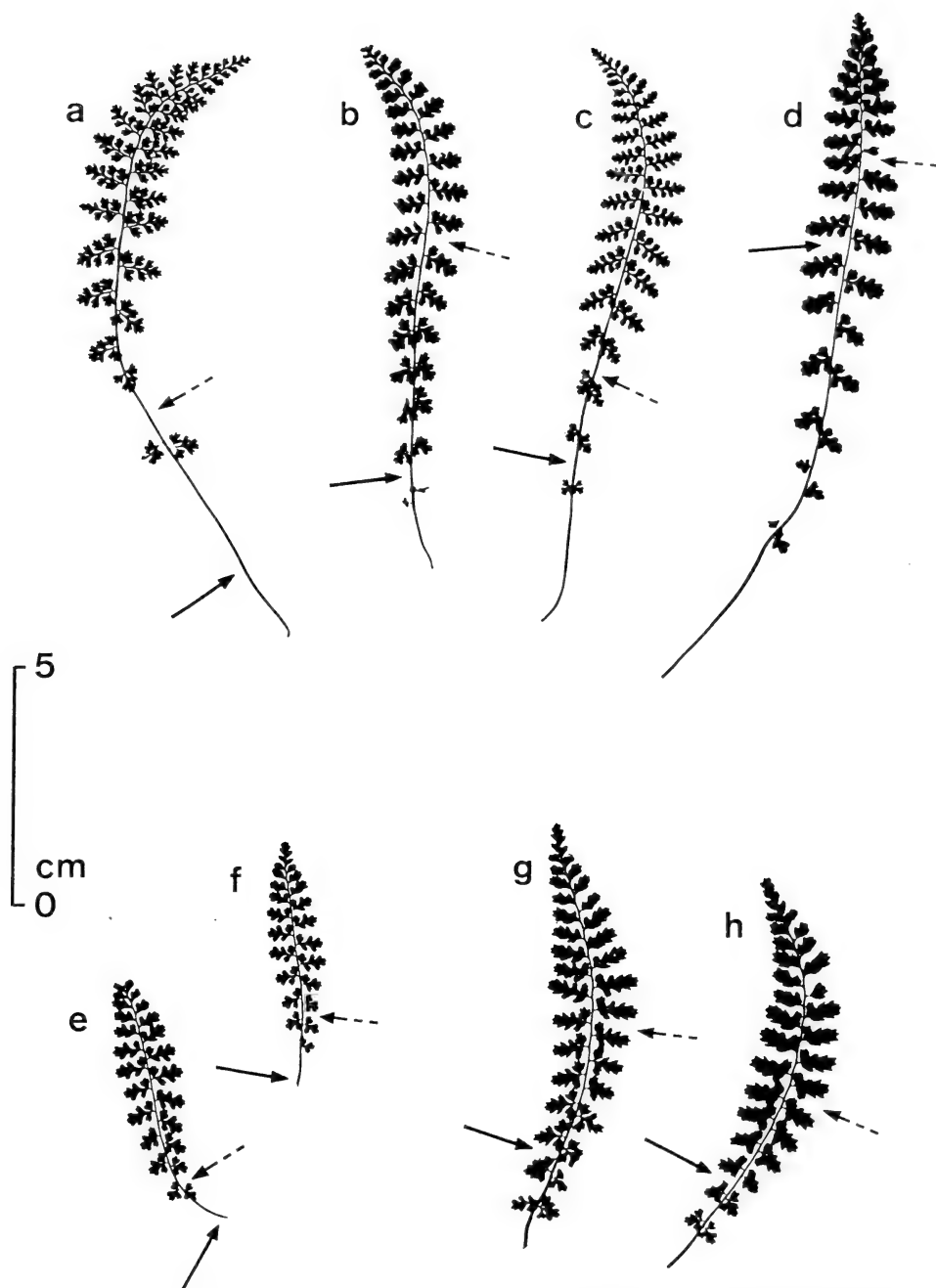


FIGURE 2. *Asplenium x reichsteinii*, its parents and the artificially produced hybrid *Asplenium majoricum* x *A. fontanum*; silhouettes of fronds; a: *Asplenium fontanum*; Gorge du Verdon, Dept. Var, France; WB 52/72, 3.4.1972; b, c: *Asplenium x reichsteinii*; Biniaraix near Sóller, Mallorca, Spain; Ras-535, 13.10.1986; d: *Asplenium majoricum*; Puig d'en Barrera near Sóller, Mallorca, Spain; WB 167/71, 10.4.1971; e, f: *Asplenium x reichsteinii*; Biniaraix near Sóller, Mallorca, Spain; WB 46/86, (= SP 24/86) 17.4.1986; g, h: Synthesized hybrid between *Asplenium majoricum* q (Sóller, Mallorca x *A. fontanum* ♂ (Roche, Switzerland; AS 266 (i), 30.5.1962. The arrows indicate the position where the colour of the rachis or of the stipe changes from brown below to green above. As this position is different on both surfaces solid arrows were used as markets for the upper surface and broken arrows for the lower surface.

Paratypes: A second plant of *Asplenium x reichsteinii* was discovered on the same day (17.4.1986; leg.: H.W. Bennert et U. Peters) somewhat above (c. 200m alt.) the locality of the holotype. This plant is in cultivation in Bochum (as SP 24/86); fronds of it will be deposited in the following herbaria: BM, G, K, MA and Z. A third plant collected on 13 October, 1986 (leg.: H.W. Bennert, H. Rasbach et K. Rasbach) was divided into two parts both being cultivated in Basel (as TR-6540 a & b). Of a fourth plant (that remained in the field) fixations were made and fronds were collected on 13 October, 1986; these are kept in the private herbaria of H. and K. Rasbach (Ras-535) and H.W. Bennert (WB 71/86). The cytological examinations that were made of all paratype plants gave the same results as in the case of the holotype.

Hybrid plant with its gross morphology being intermediate between both parents, however rather similar to *Asplenium fontanum* from which it can be distinguished by the following characters. Pinnae more compact and less deeply cut; pinna segments less sharply toothed. Stipe and lower part of the rachis (especially on the abaxial surface) dark brown coloured. Scales of rhizome in their colour intermediate between the parent species (in *Asplenium fontanum* light brown, in *Asplenium majoricum* deep brown). Fronds (of the wild growing plants) up to 12cm long and 1.5cm broad. Spores abortive (Fig. 3). Plant triploid with 36 bivalents and 36 univalents at meiosis.

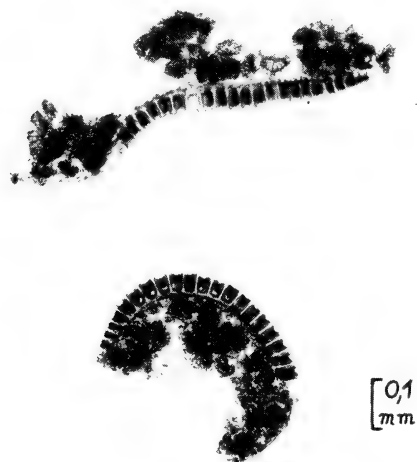


FIGURE 3. Ripe sporangia of *Asplenium x reichsteinii* containing aborted spores.

CYTOLOGY AND ORIGIN OF *ASPLENium X REICHSTEINII*

The morphology of *Asplenium x reichsteinii* clearly suggests a relationship to *Asplenium fontanum* and *Asplenium majoricum* (see Fig. 1 and Fig. 2). Further support for this interpretation comes from the cytological results. As *Asplenium x reichsteinii* is triploid it must have originated from a cross between a tetraploid and a diploid species. The pairing behaviour of chromosomes showing 36 bivalents and the same number of univalents at meiosis (Fig. 4) can be interpreted in two different ways. One possibility is that an autotetraploid (AAAA) and an unrelated diploid species (BB) were involved with the bivalents originating from the autotetraploid species exclusively (AAB). The same pairing behaviour may result, however, if an allotetraploid species (AABB) and a diploid species containing a related genome (AA or BB) hybridize; in this case each species contributes one set of chromosomes to the bivalents observed at meiosis (AAB or ABB).

Considering the first possibility *Asplenium trichomanes*, *A. petrarchae* and *A. ruta-muraria* are the autotetraploid species, *Asplenium fontanum* (see following chapter) and *A. onopteris* L. the diploid ones that occur in the vicinity of Söller thus representing possible candidates involved in hybridization. None of the hybrid



FIGURE 4. Cytology of *Asplenium x reichsteinii* (type plant WB SP 43/86): a: Photograph of spore mother cell during meiosis (diakinesis) showing 36 bivalents and 36 univalents; b: Explanatory diagram; bivalents black, univalents in outline; preparation by H.R.

combinations between these species would, however, result in a plant exhibiting such an *Asplenium fontanum*-like morphology as *Asplenium x reichsteinii* does. Even hybrids involving *Asplenium fontanum* should show closer morphological relationships to the tetraploid parent as the latter would contribute two sets of chromosomes which would dominate over the single set coming from *A. fontanum*.

When checking the second possibility of explaining the cytological results only one allotetraploid species has to be considered, namely *Asplenium majoricum*. Keeping in mind that it contains two genomes of *Asplenium fontanum* and *A. petrachae* (FoFoPePe, see introduction) only a cross involving *Asplenium fontanum* (FoFo) or diploid *A. petrachae* (PePe) would show the pairing behaviour observed. Apart from the fact that diploid *Asplenium petrachae* is to date not known to occur on the Balearic Islands the hybrid involving this species (FoPePe) should be close to *A. petrachae* in its morphology. The only hybrid combination to remain is that between *Asplenium majoricum* and *A. fontanum*. This hybrid must be triploid and have the genome formula FoFoPe with one genome Fo being derived directly from the diploid parent *Asplenium fontanum* and the other one being contributed by *A. majoricum*. This indeed explains both the morphological features (two genomes Fo dominate over one Pe) as well as the cytology (the bivalents being formed by the two genomes Fo) of *Asplenium x reichsteinii*.

Though this interpretation of the origin of *Asplenium x reichsteinii* hardly can be doubted it is, for reasons that will become obvious in the following chapter, of considerable value to obtain further support from independent investigations. In order to elucidate the origin and interrelationships of *Asplenium majoricum*, Sleep (1967) produced hybrids in various combinations. Within her hybridization programme she successfully synthesized the hybrid between *Asplenium fontanum* and *A. majoricum*. For this plant she reports exactly the same pairing behaviour of chromosomes as observed in *Asplenium x reichsteinii*. Furthermore, the morphology of this artificially produced hybrid is almost identical with that of *Asplenium x reichsteinii* from Mallorca (Fig. 2). The only obvious difference is that in the extension of the brown colour of the rachis (which especially in hybrids may vary to some extent). The two fronds of the synthesized hybrid that are shown in Fig. 2, g and h, will be deposited in B together with the holotype.

ON THE OCCURRENCE OF *ASPLENIUM FONTANUM* ON MALLORCA

Asplenium majoricum as one parent species of *Asplenium x reichsteinii* is rather frequent in the area where the hybrid plants were found. To our surprise not even a single plant of *Asplenium fontanum* could be discovered although several days were spent investigating the fern flora around Sóller with special attention given to the occurrence of this species. In modern literature *Asplenium fontanum* is consistently listed as a rare but undoubted member of the Majorcan flora (Jalas & Suominen 1972, Bonafè 1977, Duvigneaud 1979, Pichi Sermolli 1979, Greuter et al. 1981, Bolòs & Vigo 1984, Salvo et al. 1984, Smythies 1984, Castroviejo et al. 1986). Nevertheless, any authentic and reliable recent report that would confirm the present occurrence of *Asplenium fontanum* on Mallorca seems to be lacking. Judging from the information given by Bonafè (1977) all corresponding original reports date back to the time before 1920. The oldest source that mentions *Asplenium fontanum* from Mallorca seems to be the catalogue of vascular plants of the Balearic Islands by Marès & Vigineix (1880). At that time *Asplenium majoricum* had not yet been described as a separate species; this was done by Litardière in 1911. Therefore it seems doubtful whether really *Asplenium fontanum* and not *A. majoricum* was meant. In his chapter on *Asplenium fontanum* Bonafè (1977) also mentions the existence of herbarium specimens and

presents a photograph (p.34) showing a complete dried plant being kept in the "Herbari Bianor de Palma". This voucher could indeed belong to *Asplenium fontanum*. Bonafè (1977) further reports that specimens obviously belonging to the same collection are kept in the herbarium of the Botanical Institute at Barcelona. The sheet with these specimens (no. 72095) was borrowed from Barcelona and thoroughly examined. On the basis of morphology (shape of pinnae, green colour of stipe and rachis) and the well developed (not aborted) spores with an exospore length of (29-)32-35(-41) μ m it is obvious that these plants indeed represent true *Asplenium fontanum* (Fig. 5). The



FIGURE 5. Herbarium specimen of *Asplenium fontanum* from Sóller, Mallorca, kept in the herbarium of the Botanical Institute at Barcelona (no. 72095). Leg.: F.re Bianor-Marie; 15.11.1917. Silhouette of whole plant.

inscription on the label is as follows: "Plantes des Balears *Asplenium Halleri*, R.Br. Murs des olivaiés. Soller, Est. 1917, 15 Novembre. F.re Bianor-Marie". This find was obviously the basis for the report of *Asplenium Halleri* (a synonym for *Asplenium fontanum*) in the plant list of Bianor (1917). Although he does not mention *Asplenium majoricum* (which by that time had already been described as a separate species) Bianor's statement must be accepted as correct. More recently collected specimens in the private herbarium of J. Orell, Palma de Mallorca, with a morphology close to *Asplenium fontanum* were checked and found to belong to *Asplenium x reichsteinii* (see following chapter).

If *Asplenium fontanum* still exists on Mallorca it must be a very rare species possibly restricted to one or very few localities, with only a small number of individuals. We are inclined to believe that it would not primarily grow on the walls of the olive terraces as *Asplenium majoricum* and *A. petrarchae* do but prefer more favourable microhabitats on limestone cliffs. These should be shady and moist to ensure a relatively good water supply especially during summer time when long lasting rainless periods appear which are typical of the Mediterranean climate. Such habitats are more likely to occur at higher elevations in the mountains where as a consequence of frequent cloud formation air humidity tends to be high and water may condensate thus improving plant water relations. *Asplenium fontanum* is certainly less drought

resistant than *Asplenium petrarchae* and *A. majoricum* or other members of this genus.

Although we could not establish the present occurrence of *Asplenium fontanum* on Mallorca there is good reason to believe that it was, and is, still there. One argument is that *Asplenium fontanum* is one parent species of *A. majoricum* and it is most probable that the latter originated on Mallorca where it is endemic. The second point is the rather frequent occurrence of *Asplenium x reichsteinii* (see following chapter). The normal situation for fern hybrids to arise is that both parent species are present often growing closely together. The tendency of *Asplenium x reichsteinii* to occur at somewhat higher elevations (around 200m alt., highest locality at 235m alt.) and its preference for natural limestone cliffs (only 2 out of 6 plants grew on walls), always at the base of steep and high projecting rock faces, are remarkable and may be indicators for the habitats where *Asplenium fontanum* can be expected on Mallorca.

EARLIER REPORTS ON HYBRIDS BETWEEN *ASPLENIUM FONTANUM* AND *A. MAJORICUM*
The oldest published report on hybrids between *Asplenium fontanum* and *A. majoricum* seems to be that by Sleep (1967). As already mentioned she produced this cross artificially within a hybridization programme to study the origin of *Asplenium majoricum*. Under the applied experimental conditions it formed rather easily (6.4% success).

Besides these artificially raised hybrids one wild plant that was found near Sóller by Schulze, Orell and Bonafè in 1964 (det. 24. III. 1964) obviously represents the cross between *Asplenium fontanum* and *A. majoricum*. This plant is referred to in several publications (Jaquotot & Orell 1968, Lovis & Reichstein 1969, Bonafè 1977, Reichstein 1981, Castroviejo et al. 1986) but without having received a valid name. Reichstein who checked pressed fronds of it (kept in the private herbarium of J. Orell, Palma de Mallorca) did not come to a final conclusion in his earlier paper (Lovis & Reichstein 1969) where he considers it as *Asplenium fontanum* or the hybrid between *A. fontanum* and *A. majoricum*. Later (Reichstein 1981), however, he stated that the assignment of Jaquotot & Orell (1968) (*Asplenium fontanum* x *A. majoricum*) is most probably correct. The fronds in the herbarium of Orell were checked again in 1986 by the present authors and only sporangia with abortive spores were found. It is therefore obvious that this plant indeed represents *Asplenium x reichsteinii*. Very recently Antoni Rebassa, a biology student living in Sóller, sent 2 fronds of another plant of *Asplenium x reichsteinii* collected in October 1986. He describes the locality where he found the hybrid as follows: "Son Vencis", Ses Tres Creus, Sóller. This is probably the same area where Schulze, Orell and Bonafè found their plant in 1964.

This means that until now at least 8 different individuals of *Asplenium x reichsteinii* have been found in nature. As the hybrid resembles *Asplenium majoricum* it may easily be overlooked unless it is examined closely. Therefore more hybrid plants are to be expected and may be discovered in the neighbourhood of Sóller.

ACKNOWLEDGEMENTS

We thank Dr A. Sleep, Leeds, for providing us with two very valuable fronds of the artificially produced hybrid between *Asplenium fontanum* and *A. majoricum*, Mr J. Orell, Palma de Mallorca, for letting us examine his specimen of *Asplenium x reichsteinii*, Prof. Dr T. Reichstein, Basel, for careful cultivation of the type plant and Dr J. Montserrat, Barcelona, for sending us the voucher of *Asplenium fontanum* from Mallorca on loan. Furthermore we gratefully acknowledge the help of Prof. Dr H. Haeupler, Bochum, who not only gave some information on floristic literature of the Balearic Islands but also enabled one of us (W.B.) to spend two days in the Sóller area during a students' excursion to Mallorca in April 1986. Our thanks are extended to Dr

B.S. Parris, Kew, Prof. Dr K.U. Kramer and Dr J.J. Schneller, both Zürich, for reviewing the manuscript and correcting our English; Prof. Dr K.U. Kramer also improved the Latin diagnosis. We are also grateful to Mrs I. Künzel, Bochum, who assisted us with the photographic work.

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REVIEW

INDEX OF THELYPTERIDACEAE by J. W. Grimes and B. S. Parris. 50 pp. 154 x 243mm. Royal Botanic Gardens, Kew. ISBN 0 947643 03 6. 1986. Price £6.30 (over the counter) or £7.25 (incl. p. & p) from Dr B.S. Parris at R.B.G., Kew, Richmond, Surrey, TW3 3AE.

This slender book consists of an easily referable index, in the form of three columns across the page. The first column is an alphabetical arrangement of all the basionyms of species which are now included in the Thelypteridaceae. Column two gives the genus, author and date in which that epithet was originally described; column three gives the present (or proposed) disposition, with author and date when published, or in the case of synonyms, the accepted species name, which may then be looked up in column one. For full bibliographical references one must refer to *Index Filicum*; all modern taxonomic treatments, up to the end of 1985, have been covered.

Thelypteridaceae is a large and confusing group and such an index cannot be final. We are promised alterations and additions in the future in the form of Supplements. As pointed out in the Introduction, opinions will differ and there are doubtless some mistakes or omissions. I am sure they will be few. This little book, well bound in a soft, but durable, plastic-impregnated cover, is a sensible and very useful spin-off of herbarium curation.

A.C. JERMY

NOTES ABOUT *ASPLENIUM* I. *ASPLENIUM QUEZELII*, A PSEUDO-ENDEMIC SPECIES IDENTICAL WITH *A. DAGHESTANICUM* (ASPLENIACEAE : PTERIDOPHYTA)

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ABSTRACT

A comparative morphological study has shown that *A. quezelii* and *A. daghestanicum* are identical. *A. daghestanicum* is a relic (caucasian) element of the Tibesti flora, with close relatives in the Himalayas and China.

With great pleasure I dedicate this article to Prof. T. Reichstein. We have been working together to get a better understanding of various "difficult" *Asplenias*. Reichstein's interest in this genus is illustrated by the 27 articles he wrote about it in the last 25 years. The discovery of some new species in the Himalayas and China, similar to *Asplenium daghestanicum* Christ and *A. quezelii* Tardieu-Blot, renewed our interest in this group. Several new species await description. This paper only deals with the identity of *A. daghestanicum* and *A. quezelii*.

INTRODUCTION

H. Christ described *A. daghestanicum* in 1906 from a single collection (5 plants) made by Alexcenko and Woronow (holotype : P !, isotype : BR !). The ferns were collected in 1902 near Kurag in Daghestan (NW Caucasus). Christ suggested some distant relationship with *A. fontanum* Bernh., but *A. daghestanicum* became almost forgotten until Reichstein et al. (1973) compared it with *A. creticum* Lovis, Reichst. & Zaffran. At Reichstein's request Askerov collected the species again, in the same area, in 1982. Spores of this collection were used to raise progeny (TR-6062) for cytological studies (Askerov et al. in prep.). Until now, *A. daghestanicum* was considered to be an endemic of Daghestan.

In 1956 P. Quézel collected the single plant that Mme. Tardieu-Blot (1958) described as *A. quezelii*. It came from Mt. Emi-Koussi in the Tibesti massif of northern Chad (Sahara desert). She compared her new species only with *A. lepidum* Presl, a distantly related south European fern. *A. quezelii* was also mentioned by Reichstein et al. (1973), and compared with *A. creticum*. Most later authors (Quézel (1971 : 448 & 1983 : 414), Ozenda (1977 : 524)) have followed Tardieu-Blot's species concept (= an endemic of the Tibesti plateau, related to *A. lepidum*).

Since *A. daghestanicum* and *A. quezelii* look very similar, a comparative morphological study, including macro- and micro-characters, was undertaken to establish whether they were closely related or conspecific.

MATERIALS AND METHODS

The following collections were studied:

- A. daghestanicum* – Alexcenko et Woronow 450, U.S.S.R., Daghestan, Kurinski District, near Kuraeg, 21-V-1902. (Holotype P !, iso BR !).
- A. daghestanicum* – Askerov s.n., U.S.S.R., Daghestan, 2200m. 1982 (LE !).
- A. daghestanicum* – Reichstein 6062 (TR 6062), cultivated progeny of Askerov s.n., Basel (GENT, pers. herb. T. Reichstein).
- A. quezelii* – Quézel s.n., Chad, Tibesti, Emi-Koussi, lappiaz volcaniques du flanc NW, 3300m, 1956. (Holotype P !).

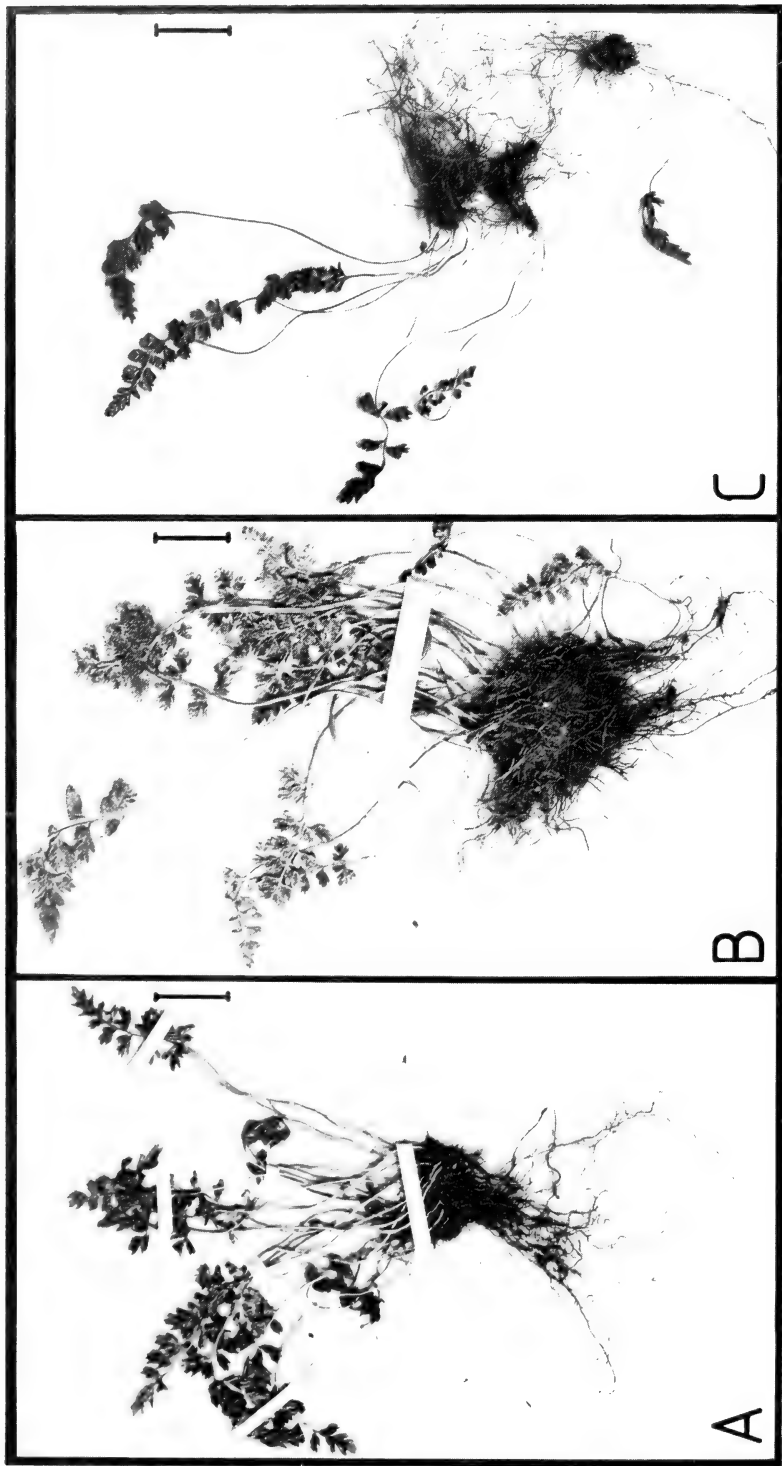


FIGURE 1. A: *A. quezelii* (Quézel s.n., holotype, P); B, C: *A. daghestanicum*. (B: Alexcenko et Woronow 450, holotype, P; C: Askerov s.n., LE). Bar = 1 cm.

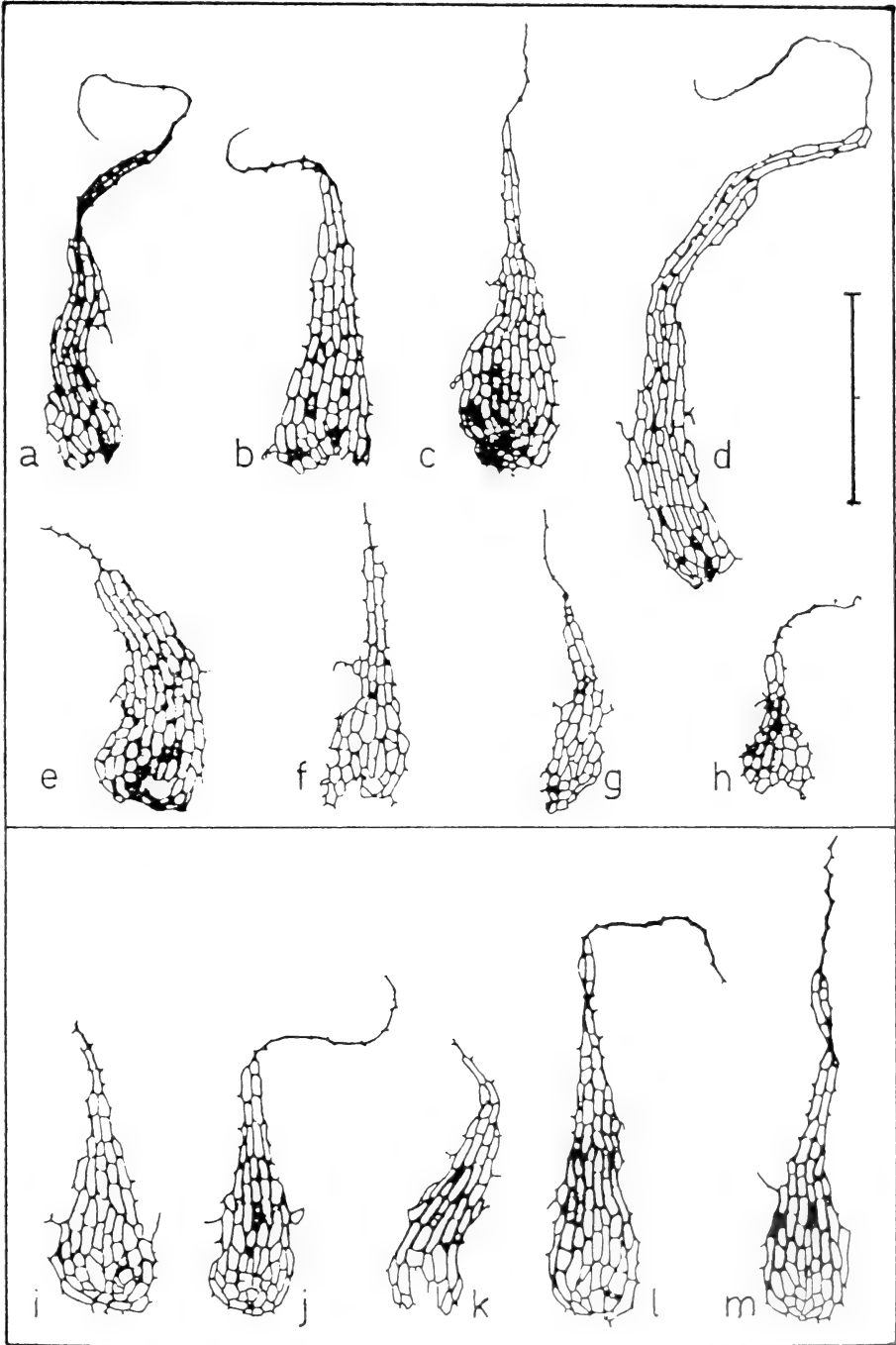


FIGURE 2. Paleae. *A. daghestanicum* [Alexcenko et Woronow 450; (a : holo-, b : isotype); Askerov s.n. (c,d,f-h); TR 6062 (e)], *A. quezelii* [Quézel s.n.-holotype (i-m)]. Bar = 1 mm.

Epidermis preparations were made and studied following standard procedures (Viane 1985); SEM investigations were done on untreated spores coated with gold. All micromorphological characters used are mentioned in Table 2. Stomatal terminology is according to Van Cotthem (1970).

RESULTS

Macromorphological analysis

The overall habit of the plants studied is the same (Fig. 1): all have a short oblique to upright rhizome, with several fronds close together at the top. The paleae (rhizome and stipe base) of both species are identical (Fig. 2); clathrate, without a central dark line, and with a few marginal outgrowths, there are no large size differences (1.5-3mm long x 0.4mm wide) between the specimens. The leaves (3-7cm long) have a stipe about twice as long as the lamina (1.5-2.5cm long x 1cm wide), which is bipinnate only at the base. The pinnae, gradually reduced towards the confluent apical segment, are a little longer than broad; their dorsal surface is often obscured with sporangia. The indusia (0.8-1.5mm x 0.4mm) have an entire to slightly undulating edge. Table 1 gives the mean values and ratios for the macroscopical characters studied; all collections closely agree. The only discordant element is the short stipe of the cultivated plant (TR-6062); the reduction of the stipe length is an apparently very common effect of cultivation (compare values from the original, wild (Askerov) collection with these of TR-6062 (its progeny)).

Micromorphological analysis

The pattern of the epidermis cells is so similar for all collections that only that of the holotypes is illustrated (Figure 3). Stomates, of the polocytic type, have guard cells 40-50 μ m long. The polocytic cell, this is the cell surrounding the guard cells distally, is always a little wider than long. The exospore length is 30-36 μ m, which indicates, just as the guard cell size, that the specimens are probably tetraploid. All microcharacters studied are on Table 2; it is clear that none of the collections can be separated from the set on microscopical grounds.

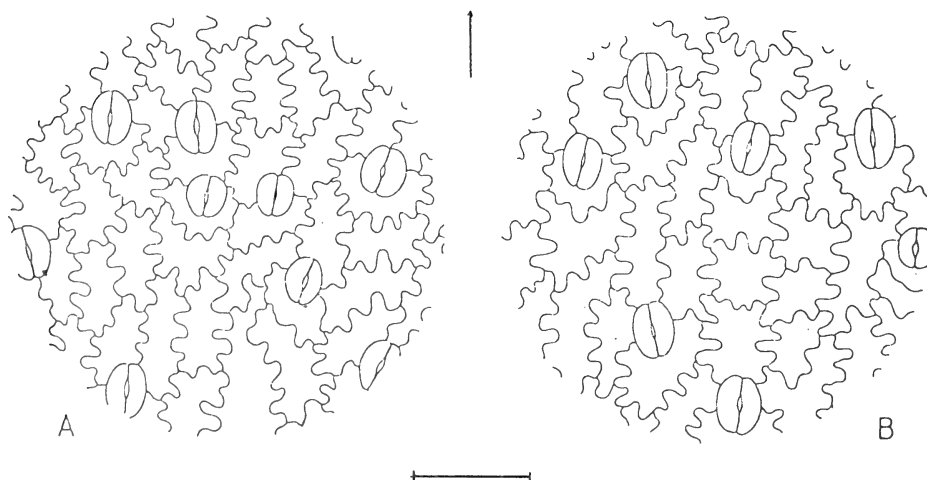


FIGURE 3. Epidermal cell patterns : A : *A. daghestanicum* (holotype); B : *A. quezelii* (holotype). Bar = 100 μ m; arrow indicates direction of vein towards leaf margin.

Scanning electron microscopy (SEM) of spores can often be used to distinguish closely related taxa (e.g. *Asplenium adiantum-nigrum* L. from *A. cuneifolium* Viv. and *A. onopteris* L.; *A. fontanum* ssp. *fontanum* from *A. fontanum* ssp. *pseudofontanum* (Koss.) Reichst. & Schneller; etc.). SEM of *A. daghestanicum* and *A. quezelii* spores (Fig. 4) revealed that these are so similar that they cannot be used to separate the species, not even on a subspecific or varietal level.

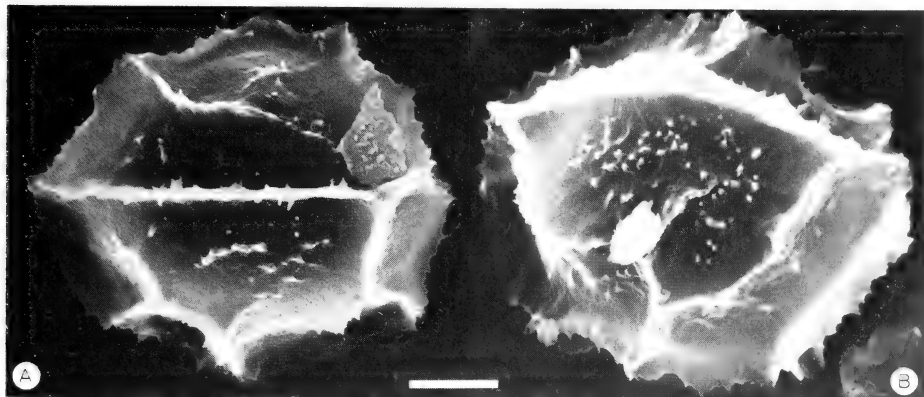


FIGURE 4. SEM spore picture of *A. daghestanicum* (A); and *A. quezelii* (B). Bar = 10µm.

Conclusion

The conclusion of this morphological study is that *A. daghestanicum* and *A. quezelii* are the same species. The correct name must then be *A. daghestanicum*, as Christ's binomial is the oldest legitimate one; *A. quezelii* Tardieu-Blot is hereby reduced to a (taxonomical) synonym.

DISTRIBUTION AND RELATIONSHIPS

Until now, both *A. daghestanicum* and *A. quezelii* were considered endemics, the former of Daghesian and the latter of the Tibesti massif. Following Tardieu-Blot's (1958) description and statements about the supposed affinities of *A. quezelii* with the south european *A. lepidum*, most later authors have copied her in their phytogeographic papers [a.o. Knapp (1973 : 425); Ozenda (1977 : 523); Quézel (1971 : 448, 1983 : 414) etc.]. In a critical article Lebrun (1983) showed that the number of true endemic species (12) from the Saharan mountains is considerably lower than had been estimated (85). Now *A. quezelii* can also be added to his list of so-called pseudo-species (= pseudo-endemic species).

The former considerable phytogeographic interest of *A. quezelii* is not lessened now that it is included in *A. daghestanicum*. At present it is only possible to consider the African population as a Caucasian element in the Tibesti flora; it (both) probably is (are) relic(s) of a flora that was present under much wetter conditions. The author does not know of any other plant with a similar disjunct (3800km) distribution.

A. daghestanicum is related to a number of (partly undescribed) small ferns, best represented in the Himalayas and China (a.o. *A. kongashanense* Ching, *A. subdigitatum* Ching, *A. xinjiangense* Ching). Some new species belonging here will be described in the near future (Reichstein et al. in press). In the meantime, plant collectors in the Mediterranean to S.E. Asia are asked to look out for these rather small, easily overlooked ferns.

TABLE 1. Mean values (in mm) and ratios of macromorphological characters.
 Lt = total leaf length; S = stipe length; La = lamina length; W1 = lamina width; N = number of pinnae; Lpal = paleae length;
 Wpal = paleae width; Lpi = pinnae length; Wpi = pinnae width; Lso = sorus length; Wso = sorus width.

Collection	Lt	S	La	La/S	W1	La/W1	N	Lpal	Wpal	Lpal/Wpal	Lpi	Wpi	Lpi/Wpi	Lso	Wso	Lso/Wso
Alexcenko & Woronow 450 (BR)	44	28	16	0,6	7	2,3	5	2,4	0,4	6	3,9	3,5	1,1	1,0	0,4	2,5
Alexcenko & Woronow 450 (P)	64	44	20	0,5	9	2,2	5	2,4	0,4	6	4,0	3,9	1,0	0,9	0,4	2,3
Askerov s.n. (LE)	54	37	17	0,5	9	2,0	5	1,8	0,4	5	4,5	3,5	1,4	1,3	0,4	3,2
TR 6062 (GENT)	35	14	21	1,6	9	2,3	6	2,0	0,4	5	3,7	3,2	1,2	1,0	0,4	2,6
Quezel s.n. (P)	55	36	19	0,5	9	2,1	5	2,1	0,4	5	4,1	3,8	1,1	1,1	0,4	2,7
Overall mean \pm stand. deviation	50 ± 11	32 ± 11	19 ± 3	0,5 $\pm 0,1$	9 ± 2	2,2 $\pm 0,4$	5 ± 1	2,1 $\pm 0,5$	0,4 $\pm 0,1$	5 ± 2	4,0 $\pm 0,6$	3,6 $\pm 0,8$	1,2 $\pm 0,3$	1,1 $\pm 0,3$	0,4 $\pm 0,1$	2,6 $\pm 0,7$

TABLE 2. Mean values (in μ m) and ratios of micromorphological characters.
 Lst = guard cell length; Wst = stomata width; Lpolo = length polycytic cell; Wpolo = width polycytic cells;
 Lepc = length epidermal cells; Wepc = width epidermal cells; l = depth of lobes of epidermis cells;
 Lexo = length of exospore; Wexo = exospore width.

Collection	Lst	Wst	Lst/Wst	Lpolo	Wpolo	Lpolo/Wpolo	Lepc	Wepc	Lepc/Wepc	l	l/Wepc	Lexo	Wexo	Lexo/Wexo
Alexcenko & Woronow 450 (BR)	43	33	1,3	77	82	0,9	104	62	1,7	19	0,3	32	27	1,2
Alexcenko & Woronow 450 (P)	46	33	1,4	67	76	0,9	92	52	1,8	19	0,4	33	25	1,3
Askerov s.n. (LE)	42	31	1,4	67	73	0,9	102	48	2,1	19	0,4	33	25	1,3
TR. 6062 (GENT)	42	34	1,2	67	70	1,0	104	51	2,1	18	0,4	33	26	1,3
Quezel s.n. (P)	49	33	1,5	69	80	0,9	104	58	1,8	19	0,3	34	27	1,3
Overall mean \pm stand. deviation	44 ± 4	34 ± 4	1,3 $\pm 0,1$	68 ± 7	74 ± 9	0,9 $\pm 0,1$	101 ± 13	52 ± 9	2,0 $\pm 0,4$	18 ± 3	0,4 $\pm 0,1$	33 ± 2	26 ± 2	1,3 $\pm 0,1$

ACKNOWLEDGEMENTS

I thank the Directors and Curators of BR and P for the loan of valuable type material. Prof. Reichstein supported and encouraged my work in many ways; he also cultivated and provided material of the Askerov collection. Ir. Bohyn made the SEM available. I thank Prof. Van Cotthem and Prof. Van der Veken for supporting my research at their laboratory. I am grateful to Dr. Mary Gibby for organizing this special anniversary issue and for revising the English text.

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REVIEW

FERNS AND ALLIED PLANTS OF VICTORIA, TASMANIA AND SOUTH AUSTRALIA by Betty D. Duncan and Golda Isaac. 258 + xii pp., 246 figures, 92 maps, 8 plates, 185 x 255mm. Melbourne University Press. ISBN: 0 522 84262 3. Price £25.00.

This book is a welcome addition to the ranks of fern floras and certainly lives up to the claim on its dust cover to be of use to naturalists, botanists and gardeners. It is intended to be used primarily as an aid in the field identification of ferns and fern allies. Two keys to genera are provided. The first is a tabular key for fertile material which is conveniently printed on a single fold out page. The second is an illustrated dichotomous key for fertile and sterile specimens. Within each genus there is a key to species and these keys, together with detailed descriptions of each species, clearly indicated field characters and good black and white photographs or drawings of whole fronds or complete plants (and sometimes more detailed illustrations of rhizomes, scales and fertile parts of the frond) should enable anyone to make correct identifications. The colour plates provide additional important information on habit, habitat and frond colouration; they are of the same high quality we have come to expect from recent Australian fern books. Distribution maps are included for most of the species which occur in the state of Victoria and much useful ecological information is provided. For the gardener there are guidance notes on situation requirements and suitability for pot, basket or rockery cultivation, while the broader principles, both of propagation by vegetative means and by spores, and of fern growing in general, are dealt with in the final chapter by C.J. Goudey and R.L. Hill.

The authors are to be congratulated on their high standards of content and presentation. I highly recommend this book to anyone with an interest in Australian pteridophytes and indeed to any naturalist intending to visit south-eastern Australia. At £25.00 it is very reasonably priced.

B.S. PARRIS

**HYBRIDISATION EXPERIMENTS BETWEEN
ASPLENIUM SEELOSII AND *A. CELTIBERICUM*
 (= *A. SEELOSII* SUBSP. *GLABRUM*)
 (ASPLENIACEAE: PTERIDOPHYTA)**

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ABSTRACT

Hybridisation experiments between *Asplenium seelosii* Leybold from the Italian Dolomites and *A. celtibericum* Rivas-Martinez (= *A. seelosii* subsp. *glabrum* (Litard. & Maire) Rothm.) from N.E. Spain are described. The F_1 hybrids showed a regular meiosis ($n = 36$) and were fertile. F_2 generations were raised from two of the F_1 plants. These showed indications of recombination of factors affecting fitness. The decision by Reichstein to revert to subspecific status for the Iberian taxon is upheld.

Asplenium seelosii sensu lato is one of the strangest and most distinctive elements in the very diverse European spleenwort flora (cf. Eberle 1959, p. 66; Rasbach et al. 1968, fig. 48, p. 101). The only species to which it has even a remote resemblance is *A. septentrionale* (L.) Hoffm., with which it shares the feature of a highly reduced lamina. Indeed, it was initially regarded as a variety (var. *tripartitum*) of that species by Gustav Seelos, after whom the plant was subsequently named when described as a distinct species by Leybold (1855). (See Becherer 1962, p. 55).

Although so distinctive, *Asplenium seelosii* is nevertheless highly variable, not merely between and within populations, but also within one individual, fronds varying in morphology in response to environmental conditions, including climatic variation and season of the year. This variability is not suppressed by glasshouse culture. In these experiments, plants grew more luxuriantly in Basel than in Leeds, though the growth forms produced in Leeds were perhaps closer to those likely to be realised in the wild.

In its more luxuriant forms, the fronds of *Asplenium seelosii* consist of a relatively long stipe, terminated by a very short lamina divided into three segments, which may themselves be incised to a greater or lesser extent. The frond is rarely quite symmetrical, one of the lateral segments usually joining the axis at an appreciably lower point than the other.

The characteristic habitat of *Asplenium seelosii* is crevices of vertical limestone rock walls. Its distribution falls into two main highly disjunct areas. In central Europe, its range is based on the Italian Dolomites with outliers in Austria, N.W. Yugoslavia (Julian Alps) and Germany (just!). It occurs also in the N.E. quarter of Spain, where there are two centres — one in the eastern half of the Pyrenees (one locality here is actually in France) and the other south of the Ebro river in Guadalajara. The plant is not endemic to Europe; it occurs also in Morocco (cf. Jalas & Suominen 1972, p. 77).

The type of *Asplenium seelosii* Leybold is from the Tyrol. Unless depauperate, plants from the Dolomites (Figs. 1A-I) always have a tripartite lamina, and this lamina plainly bears numerous stalked glandular hairs. In contrast, plants from Spain are glabrous and have a less divided lamina, though it is now evident that populations vary in this latter character (Figs. 1J-S). These differences have resulted in Iberian plants being given separate taxonomic status, firstly as a variety, var. *glabrum* Litardiere & Maire (in Maire 1928), secondly as a subspecies, subsp. *glabrum*, by Rothmaler (in

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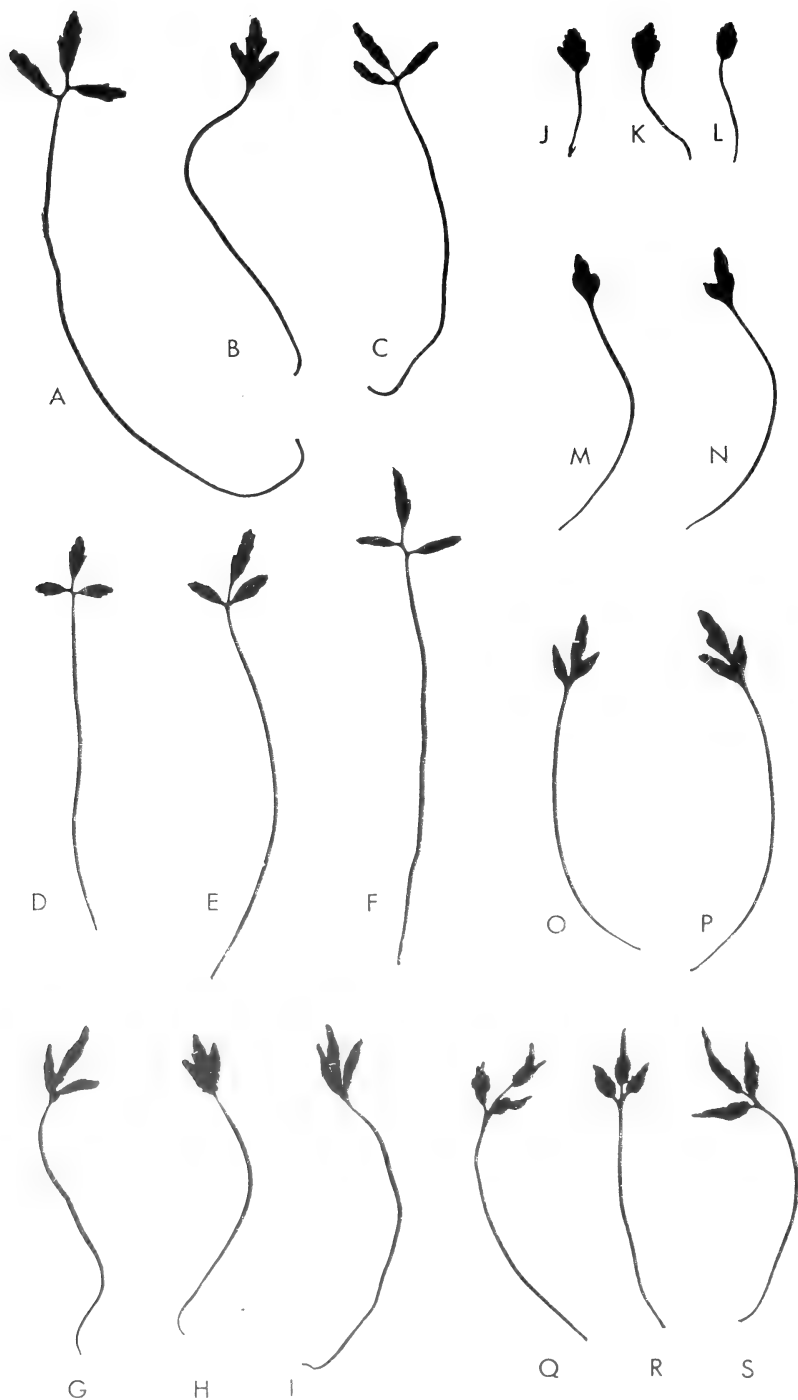


FIGURE 1. Silhouettes, $\times 0.875$, of pressed fronds of *Asplenium seelosii* (A-I) and *A. celtibericum* (J-S). A-C) Salurn, Italian Dolomites, wild collection. D-F) Buco de Vela, Italian Dolomites, cult. Leeds. G-I) Mazzin, Italian Dolomites, wild collection. J-L) progeny of isotype of *A. celtibericum*. Pinar de Campisábalos, Guadalajara, Spain, legit Rivas-Martínez et al., cult. Leeds. M & N) TR 898, N. of Orgaña, valley of R. Sègre, N.E. Spain. O & P) TR 898, cult. Basel. Q-S) TR 1193, chapel of Sta. Fee, near Orgaña, legit A. & C. Nieschalk, cult. Basel.

Cadevall & Font Quer 1937) and lastly raised to full specific rank as *A. celtibericum* by Rivas-Martinez (1967). *A. celtibericum* is based on material of extreme morphology from Guadalajara. Progeny of isotype material raised in Leeds is diminutive, with a virtually undivided lamina, consisting of only a single serrated terminal segment (Fig. 1J-L).

Both taxa are, as far as is yet known, uniformly diploid (Meyer 1957, 1967; Lovis unpub.).

It is clearly a matter of some interest to establish the degree of genetical relationship persisting between these two taxa — their origin from a common ancestor surely cannot be doubted. Accordingly, two attempts were made to hybridise them, using a characteristic though not extreme form of the Spanish plant as the male parent. The overall success obtained was 50%.

	FEMALE PARENT	MALE PARENT	FEMALE PROTHALLI	HYBRIDS
JDL 1439	<i>A. seelosii</i> Mazzin, Italy	X <i>A. celtibericum</i> Organa, Spain (TR 898)	10	6
JDL 1440	" "	X " "	10	4
			20	10

The F₁ hybrids were unexpectedly easy to discriminate from possible 'female' selfs (or stray selfed 'male' prothalli), being not only vigorous, but of distinctive morphology. They all retained the tripartite lamina of *Asplenium seelosii* sensu stricto, but were glabrous. Thus in the F₁ hybrids division of the lamina was dominant, but glandulosity proved to be recessive. Chromosome pairing was regular, 36 bivalents being formed, as in the two parents. F₂ generations were raised from two of the F₁ hybrids. In contrast to the uniform morphology of the F₁ hybrids (Figs. 2A-E, 3A-F), the F₂ progenies (Fig. 3G-X) were variable in frond form, with some individual recombinants lying outside

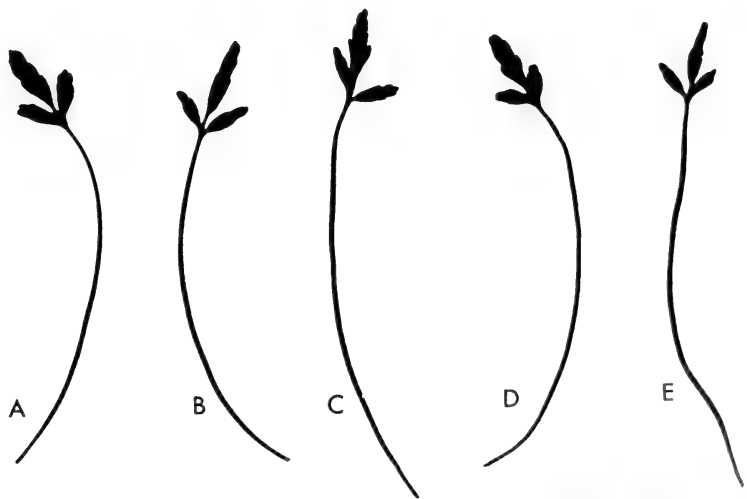


FIGURE 2. Silhouettes, $\times 0.875$, of pressed fronds of five synthetic hybrids, *A. seelosii* \times *celtibericum* (F₁), all cult. Leeds. A) JDL 1439A. B) JDL 1439D. C) JDL 1439B. D) JDL 1440B. E) JDL 1440C.

the range of the parent taxa (e.g. Fig. 3M-P). Curiously, only the sparest indications of glandular hairs were seen on the lamina of any of the F_2 plants. The suppression of glandulosity in both hybrid generations suggests that this characteristic evolved in the Tyrolean plant subsequent to its separation and divergence from the Iberian taxon and was not present in their common ancestor. The F_2 progenies also showed signs of recombination of factors affecting fitness, numerous sporophytes not surviving to maturity. Success in raising in the glasshouse a plant from so extremely specialised a habitat as that of *A. seelosii* is at best precarious, but nevertheless there is good reason to believe that, in practice, the F_2 generation shows some reduction in vigour in comparison with the F_1 . The fertility of F_2 plants was not tested.

In the light of this information, combined, I suspect, with his personal experience of the range of form present in Spanish populations, Reichstein, in his remarkable definitive review of hybrids in European Aspleniaceae (Reichstein 1981, p. 105), opted for subspecific status for the Iberian plant. Taxonomic decisions of this type can be more a matter of taste, of personal preference, rather than a question of right or wrong, but nevertheless Reichstein's decision is plainly very appropriate. Although it is true that the two areas of distribution of these taxa are so disjunct that their interfertility can have no practical effect in nature, recognition of the two taxa as geographical subspecies has the clear merit of preserving, within the classification, an indication of the close relationship that undoubtedly exists.

A remarkable diversity of form exists within the diploid taxa present in European Aspleniaceae. Using the ability to pair chromosomes at meiosis as a criterion of relationship, the great majority of inter-specific diploid combinations so far studied show no evidence of affinity. This can be true (e.g. *trichomanes* x *viride* : 72 univalents) or virtually so (e.g. *cuneifolium* & *onopteris* : 0 - 6 bivalents*), even where some evidence of affinity might be expected on morphological grounds. In contrast, *A. seelosii* x *celtibericum* shows us a situation where geographical isolation exists, accompanied by some morphological differentiation, but divergence is not yet sufficient to affect chromosome pairing.

It would be of great interest to investigate certain other pairs of diploid species of *Asplenium*, namely 1) *A. jahandiezii* (Litard.) Rouy and *A. bourgaei* Boiss. ex Milde, and 2) *A. aegaeum* Lovis, Reichst. & Greuter & *A. fissum* Kit. ex Willd. *A. jahandiezii* is restricted to the vicinity of the Gorge du Verdon in S.E. France, whereas *A. bourgaei* is a plant of Asia Minor, principally Asian Turkey. Their morphology suggests a close relationship, though by no means as close as in the case of *A. seelosii* and *A. celtibericum*. Although *A. aegaeum* and *A. fissum* are unmistakable in their most characteristic forms, a few collections are difficult to place. Their distributions are approximately contiguous in the Aegaeen region. All of these four species are difficult to cultivate, and it has not yet been possible to attempt successfully to hybridise them, using the technique employed in Leeds (Lovis 1968), for which a prothallial growth sufficiently dense and vital to show, when tested, some signs of spermatozoid liberation is necessary if an hybridisation attempt is to have a reasonable chance of success. For the synthesis of such hybrid combinations, the elegant 'nearest neighbours' transplant technique devised and exploited with success in recent years by Reichstein, wherein the opportunity for hybridisation is extended indefinitely rather than restricted to a brief span in a watchglass, may well offer much better prospects.

*Evidence from *X Asplenophyllitis jacksonii* Alston (Lovis & Vida 1969), *A. x bechereri* D.E. Meyer and *A. x dolosum* Milde (Reichstein 1981, Appendix II, pp. 118 & 122). Note that tetraploid hybrids such as *A. majoricum* x *adulterinum* which show 144 univalents (Lovis & Reichstein 1969) in effect provide a demonstration of lack of ability to pair for no less than six different diploid combinations : PF, PT, PV, FT, FV & TV.

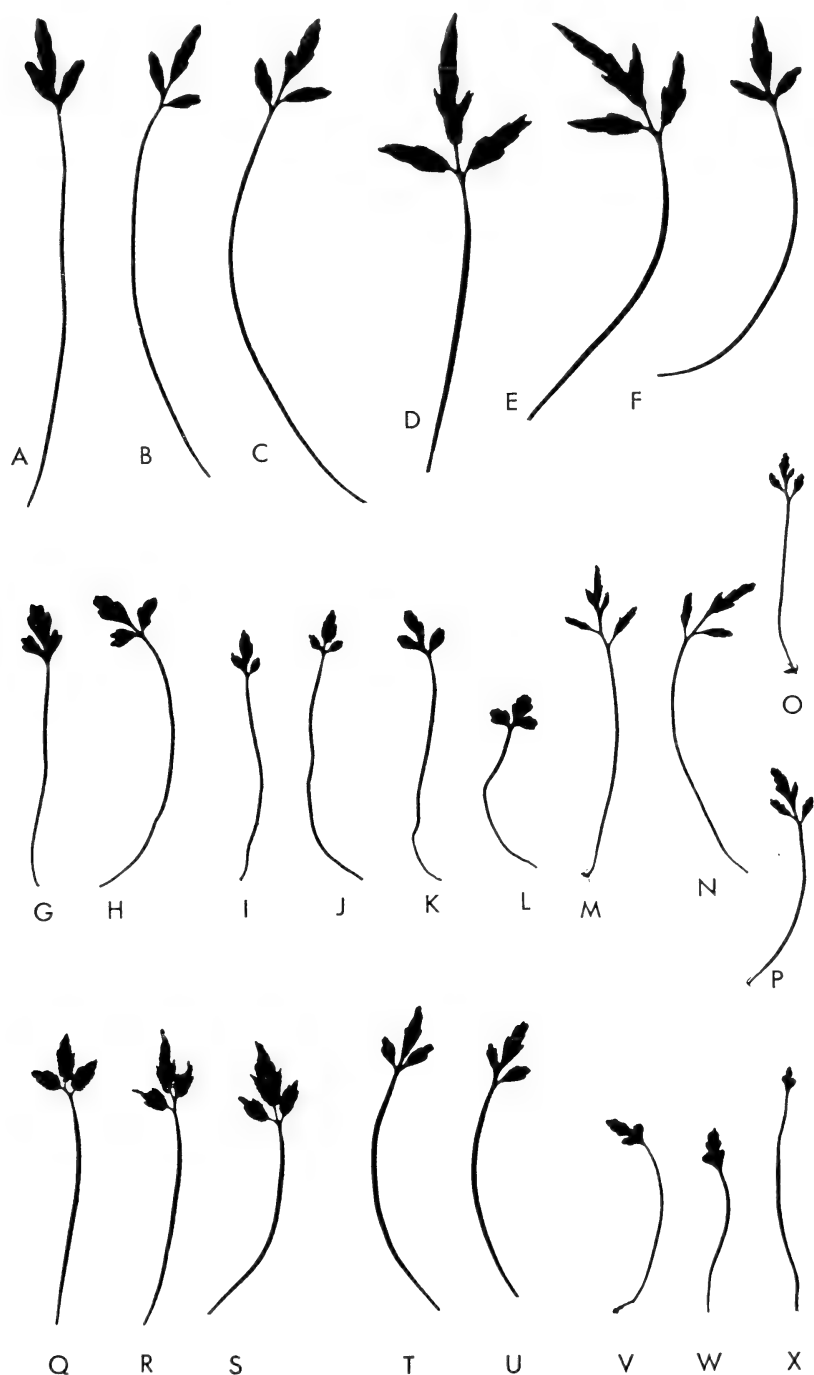


FIGURE 3. Silhouettes, $\times 0.875$, of pressed fronds of two synthetic hybrids, *Asplenium seelosii* \times *celtibericum* (A-F), and their selfed F_2 progeny (G-X). A-C) JDL 1439C, cult. Leeds. D-F) JDL 1439E (TR 1524), cult. Basel. G-P) selfed progeny of JDL 1439C, cult. Leeds. G & H) JDL 1439C:1. I & J) JDL 1439C:2. K) JDL 1439C:3. L) JDL 1439C:6. M-P) JDL 1439C:s.n. Q-X) selfed progeny of JDL 1439E, cult. Leeds. Q-S) JDL 1439E:1. T & U) JDL 1439E:2. V-X) JDL 1439E:s.n.

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It is a great pleasure and privilege to acknowledge the assistance of Prof. Dr. Tadrik Reichstein in this project, 1) in guiding me to localities of *A. seelosii* s.s., including that at Mazzin from whence the culture used as female parent was obtained, 2) for providing the material of subsp. *glabrum* subsequently utilised as male parent and 3) for cultivating in Basel, very successfully, one of the resultant F_1 hybrids.

The great increase in our knowledge of European Aspleniaceae in the last 25 years is in very large measure the achievement of one man, both directly by his own efforts, and otherwise by very materially assisting and inspiring others. This paper is dedicated to him with most grateful thanks by one who has been very fortunate in being an associate.

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OBSERVATIONS OF PROGENY OF *ATHYRIUM FILIX-FEMINA* (ATHYRIACEAE; PTERIDOPHYTA) FROM BREEDING EXPERIMENTS*

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ABSTRACT

Progeny of plants collected from natural Swiss populations have been grown for more than 8 years in a garden. The offspring resulting from intragametophytic selfing are on average much smaller and more variable in size than those from intergametophytic selfing or from crossing (out-breeding). The sporophytes originating from outbreeding were the tallest and most robust. This observation and earlier results (Schneller 1979) suggest that the genetic variability and genetic load may be very high. How is it possible to maintain so many recessive deleterious genes in natural populations? Because of the instability of the microhabitats in which the prothalli grow, soft selection may allow an accumulation of genetic load. The result of this investigation, however, can also be interpreted in light of genetic regulation, because leaf dimensions are normally controlled by polygenic complexes.

INTRODUCTION

In most homosporous ferns it is possible to breed sporophytes in three different ways: 1. intragametophytic selfing, 2. intergametophytic selfing, 3. intergametophytic crossing. In the first case completely homozygous sporophytes result, because the egg and spermatozoid are from the same prothallus and therefore genetically identical. Intergametophytic selfing implies mating gametes from two prothalli of the same parent plant. As a result totally homozygous or partially heterozygous progeny will originate depending on the mode of fertilization and the genetic composition of the parent plant. In intergametophytic crossing experiments prothalli from two different parent plants are used. In this case either homozygous plants (due to intragametophytic selfing) or heterozygous plants (degree of heterozygosity depending on the genetic constitution of the parents) result. In a study of the breeding system of *Athyrium filix-femina* (Schneller 1979) it was shown that outbreeding was most successful but intra- and intergametophytic selfing also led to progeny. The viability of the different kinds of progeny, however, was remarkably different. After 8-10 years some of the plants obtained in these earlier experiments are still alive and are growing under similar conditions. Progeny from the three different modes could be seen to be distinct. The reasons for the observed differences will be discussed.

MATERIALS AND METHODS

The parent plants were collected in Switzerland in natural populations at Horgenerberg, Horgen, Kt. Zürich (nr. A-1, A-2, A-3, A-29, A-31, A-33), at Scalasiten, Tamins, Kt. Grisons (nr. A-42, A-48, A-49, A-50), and at Göschenernalp, Göschenen, Kt. Uri (nr. A-51). The plants investigated here were experimentally produced in the years 1975-77. Since 1979 they have been grown under similar conditions in a shady garden bed in the Botanical Garden of the University of Zürich. Three classes of plants were evaluated: 1. progeny (18 plants) from intragametophytic selfing ('intra'), 2. progeny (21 plants) from intergametophytic selfing experiments ('inter'), and 3. progeny (12 plants) from crossing experiments ('cross'). In an earlier investigation

*Dedicated to Prof. Dr. T. Reichstein on his 90th birthday.

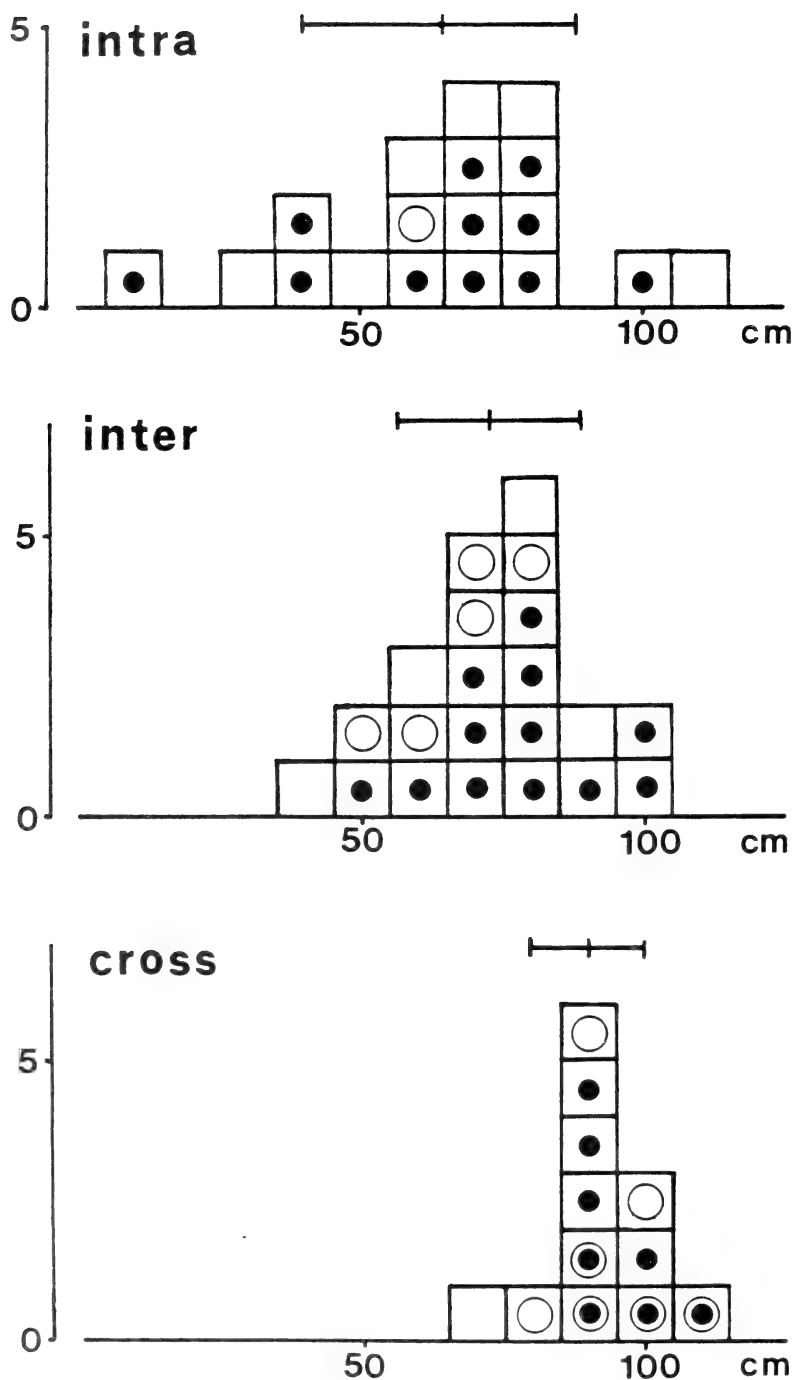


FIGURE 1. Distribution of leaf lengths of the different types of progeny. intra = intragametophytic selfing, inter = intergametophytic selfing, cross = crossing, ○ = progeny from plant A-1, ● = progeny from plant A-2, ⊙ = progeny resulting from crossing A-1xA-2, — = mean and standard deviation, blanks = progeny from plants other than A1, A2.

(Schneller & Schmid 1982) and again in this experiment it could be shown that the aspects of leaf size that determine shape are correlated. This explains why the size of the leaves was used for Figure 1. Methods for the statistical analysis of means and deviation tests follow Linder & Bechtold (1979) and Campbell (1971), SAS statistical programs (SAS Inst. 1982) were used.

RESULTS

Measurements given in Table 1 were used for the statistical comparison. The Kruskal-Wallis test showed significant differences between 'intra' and 'cross' and between 'inter' and 'cross' (SAS Inst. 1982). In Figure 1 the distribution of the leaf length is shown. The progeny of two plants (A-1 and A-2) are indicated. Principal component analysis shows significant differences between the different breeding-classes.

DISCUSSION

Earlier experiments (Schneller 1979) showed that *Athyrium filix-femina* is predominantly outbreeding. All the parent plants collected randomly from natural habitats and used for the breeding experiments were heterozygous. These original plants grew well in their original environment. They can be regarded as successful results of selection (in the past) because they survived and withstood competition. Earlier experiments (Schneller 1979) and the results presented here show that the original plants stored a remarkable amount of genetic variability. In this investigation (Fig. 1) it was shown mainly in examples A-1 and A-2 (but is true also for other examples). Because progeny are growing under similar conditions much of the observed variability is due to genetic diversity (it is difficult or impossible to distinguish in nature between the genetic component of variation and phenotypic plasticity (Schneller & Schmid 1982) because they are intermingled). Genetic variability may be expressed by advantageous, neutral, or deleterious factors. The results of breeding experiments reveal some consequences of this genetic diversity. Intragametophytic and to a lesser degree intergametophytic selfing show very different results. In many cases no sporophytes are formed. If sporophytes occur they differ strikingly. They may die at an early stage or vary in size and virility (Schneller 1979). When no sporophytes are observed this may be due to prezygotic mechanisms or to early lethal recessive genes (zygotic lethals). Dwarf or subvital sporophytes may be due to weaker recessive deleterious genes.

After nearly ten years it can be clearly seen that the three classes of progeny ('intra', 'inter' and 'cross'; Fig. 1) are distinct considering standard deviation and means of length. The differences are statistically significant with the exception of the mean leaf-length of 'intra' and 'inter' (which is significant only at the 80% level). The class 'intra' shows the largest deviation and the greatest proportion of dwarf plants. It should be noted that intragametophytic selfings have the greatest number of deaths during early stages (Schneller 1979). From the 50 original "intra"-plants only 18 survived. Even the progeny of one plant (A 1) shows a wide range of different offspring. Because the plants are homozygous, recessive genes will always be expressed. The great variance reflects genetic diversity. Dwarf or small plants could then be the result of weakly deleterious recessive genes, that may influence the metabolism of these plants. The viability of the plant and the regulation of leaf size seem to be somewhat correlated.

In the class 'inter' the deviation is smaller and the mean is larger than in the class 'intra'. This would support the hypothesis of increased heterozygosity. Heterozygosity in this case seems to have a stabilising effect on the development, i.e., some of the recessive deleterious alleles will be "masked" by dominant alleles. Some of the

recessive deleterious genes, however, will be found in homozygous condition. This would explain the still wide range of different phenotypes in this class. We can assume that the degree of heterozygosity is highest in the class 'cross'. Here we observe taller plants, a smaller variability and a greater viability. The difference between the other two origins can be explained again by the stabilising effect of heterozygosity.

In population genetics simplified models have often been used to explain the influence of genes on fitness (Sperlich 1973, Wallace 1970). The results of this investigation in my opinion cannot be explained satisfactorily by simple models.

It is obvious that genetic load (mutational and/or segregational) occurs in the gene pool of *Athyrium filix-femina*. It has to be regarded as a consequence of outbreeding. Thus, stored recessive genetic load will be a hindrance to inbreeding, mainly because lethal genes result in none or in subvital offspring that could not survive in natural conditions. Most inbred sporophytes could not compete with the crossbred ones. Fern geneticists like Lloyd (1974) and Klekowski (1982) argue that inbreeding is important for the establishment of new populations. Selection pressure for inbreeding would 'clean' the population of deleterious genes and would also have an influence on the genetic diversity. The genetic load observed in this example reflects a great genetic diversity. Is such a genetic load extraordinary for ferns (or other organisms)? We still do not know enough about how much of genetic diversity can be maintained in natural populations. The answers given by theoretical models range widely depending on the assumptions made. Looking at concrete results in ferns, Klekowski (1982) mentioned that *Osmunda regalis* has the highest load so far documented. For this species 2.39 lethal equivalents per zygote were calculated. A somewhat lower load was found in *Thelypteris palustris* (Ganders 1972). Based on my earlier results (Schneller 1979) and results of this investigation I estimate (method see Ganders 1972) a mean load of 4.87 lethal equivalents per zygote for *Athyrium filix-femina*. This is about double the load of *Osmunda regalis* (Klekowski 1982). A comparable amount of load can be found in human populations (Brues 1969).

Wallace (1970, 1975) showed that soft selection (which is density- and frequency-dependent) allows an accumulation of genetic diversity. The consequences of soft selection to genetic diversity and particularly to genetic load were calculated by Klekowski (1982). In my opinion it is the habitat of *A. filix-femina* (and of course other plants as well) that allows soft selection. It consists of a mosaic of microhabitats variable within some limits influenced by other organisms or by unpredictable physical events on the soil, such as erosion, disturbance by rain, snow, frost, cover of litter etc. The observed large genetic diversity may be partly due to the nature of the microhabitat and soft selection.

The conclusions or hypotheses made so far in this discussion were based on the assumption that the observed load is due to recessive lethal genes. We know for numerous plants that the regulation of size and shape is polygenic (Mather 1942). The different leaf sizes seen in the experiments (Fig. 1) could also be explained by the different combination of regulating genes and could be a consequence of epistasis. We still know little about either the interrelationship of structural and regulatory factors or the role of epistasis.

Finally, I am fully aware of the lack of a satisfactory explanation to the observed phenomena. But in my opinion we should focus our interest on the problems of gene regulation; some attributes we currently link with genetic load may have another cause.

ACKNOWLEDGEMENTS

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TABLE 1

intra					inter					cross				
Nr.	L	B	Ba	Pos	Nr.	L	B	Ba	Pos	Nr.	L	B	Ba	Pos
A1h1	104	14.0	7.5	10	A1i1	76	12.5	5.5	7	A1/A2-2	106	17.0	9.0	7
A1h3	78	12.0	5.5	8	A1i4	60	9.0	5.0	8	A1/A2-3	92	14.5	7.5	9
A1h4	71	10.5	5.0	8	A1i5	71	11.0	4.0	6	A1/A2-4	91	15.0	6.0	6
A1h5	12	1.5	1.0	4	A1i7	71	10.5	5.0	8	A1/A2-5	88	13.0	5.5	7
A1h6	78	11.5	5.5	7	A1i8	81	12.0	4.5	7	A1/A31-1	89	13.5	5.5	9
A1h7	67	11.0	6.0	7	A1i12	99	13.5	5.5	7	A1/A31-4	91	15.0	9.0	6
A1h8	42	6.5	4.5	8	A1i13	83	11.5	5.5	5	A1/A42-2	94	16.0	7.0	8
A1h9	58	9.5	4.0	6	A1i14	70	11.0	3.0	8	A1/A43-5	93	15.5	5.5	10
A1h10	38	5.5	2.5	7	A1i17	92	13.0	9.0	7	A2/A31-1	98	14.5	5.0	9
A1h11	71	11.5	5.5	8	A1i19	49	8.0	3.5	8	A2/A31-3	92	14.5	7.5	9
A1h12	84	10.0	6.0	9	A1i21	104	14.0	6.5	9	A2/A48-1	77	13.0	4.0	7
A2h1	60	8.5	3.0	6	A1i22	77	13.0	8.5	6	A48/A47-c	65	12.5	5.0	7
A3h5	75	13.0	5.0	7	A2i2	69	15.0	7.0	5					
A29h2	58	8.5	2.5	8	A2i3	79	13.5	4.5	8					
A33h1	109	16.5	10.5	7	A2i4	74	15.0	4.5	9					
A33h2	73	12.5	6.5	5	A2i6	64	9.0	4.0	6					
A48h3	46	7.5	3.5	7	A2i10	48	8.5	2.5	9					
A50h1	29	4.0	3.0	5	A31i1	45	9.0	4.0	5					
					A31i2	83	16.0	6.0	6					
					A50i4	59	11.0	4.5	5					
					A51i8	89	15.0	11.0	4					

TABLE 1. Leaf dimensions of progeny from different breeding experiments. intra = intragametophytic selfing, inter = intergametophytic selfing, cross = crossing, Nr. = plant number, L = length of leaf, B = breadth of leaf, Ba = length of basal pinna, Pos = position of longest pinna (basal pinna = Pos 1).

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REVIEW

ICONOGRAPHIA PALYNOLOGICA PTERIDOPHYTORUM ITALIAE. E. Ferrarini, F. Ciampolini, R.E.G. Pichi Sermolli, D. Marchetti. 1986. Webbia 40(1): 1-202. ISSN: 0083-7792.

This work is a study of the spores of the 122 species and subspecies of Pteridophytes found in Italy. The text is in Italian. For each taxa, a detailed morphological description of the spore(s) is given (a helpful glossary of the terms used, illustrated with line-drawings, is provided), with the global and Italian distributions, habitat information and cytological data. Although the (untreated) spores of all the taxa are illustrated by scanning electron micrographs, the spore measurements given are taken from dry spores (i.e. observed in air, without any mounting medium) with a transmitted-light microscope. The accounts of many of the taxa have comments on such topics as their taxonomy, nomenclature, cytology or phytogeography. A comprehensive bibliography of some 350 references is given. The new combination *Polypodium cambricum* ssp. *serrulatum* (Sch. ex Archang.) Pic. Ser. is made.

J.M. CAMUS

***ASPLENIUM TADEI* (ASPLENIACEAE : PTERIDOPHYTA), A NEW SPECIES FROM TURKEY**

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ABSTRACT

The discovery of a new *Asplenium* species, *A. tadei* Fraser-Jenkins & Schneller, is reported from Antalya province, south Turkey. Its possible relationships are briefly discussed in the light of its tetraploid cytotype, and it is concluded that it is probably an allotetraploid species, either involving *A. trichomanes-ramosum* L. and some other diploid species, possibly *A. bourgaei*, Milde or that it is a member of the *A. exiguum* Bedd., or *A. daghestanicum* Christ aggregates.

INTRODUCTION

In June 1978, while examining specimens from western Asia at Kew (K), in connection with his work on "*Flora Iranica*" (Fraser-Jenkins, Khullar & Reichstein, in prep.), the first-named author came across an unusual specimen of an *Asplenium* from Turkey, which was generally similar to *A. viride* Huds., but with an unusual frond-apex where the segments had become fused together into a terminal blade with narrow side-lobes. The specimen was unlike any other *Asplenium* species from the European area (sens. lat.) with the possible exception of *A. daghestanicum* Christ, a rare species from the eastern Caucasus, then known only from the type specimens in Paris (P), and which he had previously spent some time attempting to obtain, both in the Caucasus and by correspondence, in connection with study on that species and the closely similar, Sino-himalayan *A. aitchisonii* Fraser-Jenkins & Reichstein, by Professor T. Reichstein of Basel. However the Turkish specimen was noticeably longer, narrower and less deeply dissected than the type material of *A. daghestanicum*, and had the sori crowded towards the base of the pinnae; subsequently new material of *A. daghestanicum* brought to the BM from Dr A.N. Askerov of Baku, with the help of Prof. A. Takhtajan of Leningrad, showed that it was not the same species. The specimen concerned had been cited in the "*Flora of Turkey*" (Davis (ed.) 1965) under *A. bourgaei* Milde, a slightly similar but nevertheless markedly distinct species; its label gives the locality etc. as: "*Asplenium bourgaei*, Turkey, Vil. Antalya (Isauria), Geyik Dag, 8000', crevices of shady limestone rocks, rare. P.H. Davis 14513, 31/8/1947". It was with excitement that it was arranged for the specimen to be sent to Professor Reichstein for study as a possible candidate (at the time) for *A. daghestanicum*, or at least as something different from other European and western Asian species. On seeing it he was able to suggest that it was close to but not the same as *A. daghestanicum* and could well be a new species. However he suggested that there was also a possibility that it could be a distinctive but vicariant form of *A. creticum* Lovis, Reichstein & Zaffran, a rare allotetraploid species from Crete derived from *A. viride* and *A. aegaeum* Lovis, Reichstein & Greuter, differing from it mainly in having the distinctive fused frond-apex. In *A. creticum* the frond-apex is not normally fused but occasional small specimens can show some signs of slight fusion, though nothing like the extent that it is fused in the Turkish specimen. The latter also has a narrower and less dissected frond than *A. creticum* and the somewhat irregularly tripartite lower pinnae with the sori crowded near the base are again distinct. It was therefore reported as an *Asplenium* species near to (but distinct from) *A. creticum* by Parris & Fraser-Jenkins (1980).

In order to investigate the species further it was planned to visit the locality to search for more material, Professor Reichstein kindly agreeing to finance the excursion which was carried out in September 1979 by the first-named author along with Miss S.J. de C. Coombs.

PHYTOGEOGRAPHICAL NOTE

Geyik Dağı is part of the large area of high-level limestone shield comprising the Taurus Mountains (Toros Dağları) extending shortly inland all along the southern Mediterranean coast of Turkey and including some remote and very splendid mountains, often hard of access, such as Ak Dağ (3073m) and Bey Dağları (3086m) in the western, or Lycian, Taurus, west of Antalya, another Ak Dağ (c. 3100m), Bolkar Dağları (3240m), Aydos Dağı (3488m) and Toros Dağı (3585) in the central, or Isaurian, and eastern, or Cilician, Taurus east of Antalya and to the west and north of Adana. The shield also extends beyond the Taurus proper to Ala Dağları (3910m) to the north-east. These mountains can often be seen from a great distance as towering pale or white masses, not only because of their long-lasting snows, but also because of the very pale colour of their extensive and rugged limestone exposures. The Bey Dağları seen to the west from across the Gulf of Antalya (Antalya Körfezi), and the Bolkar Dağları seen from the north towering up above the dusty plain of Konya province (Vilhayet) are two of the best-known spectacular views of the Taurus. As one enters the mountains themselves north of Alanya, some 120km east of Antalya, the long high limestone ridge of Ak Dağ (White Mountain) comes into view, just to the south-east of which lies the connected, sharp and rugged peak of Geyik Dağı (2890m). Phytogeographically the Taurus Mountains lie within Mediterranean Turkey (see Parris and Fraser-Jenkins 1980), and form the border-line between that region and Inner Anatolia, but they are in many respects a special region themselves due to their high altitude, and as far as both ferns and flowering plants are concerned they contain not only many endemic species but also a number of extensions of the ranges of European species, sometimes as a fragmented link between the flora of Greece (via the arc from the Peloponnese, through Crete and Rhodes, and thus to the western Taurus), and the flora of the limestone regions of the south-west Caucasus. An interesting example of this turned up during the trip concerned, with the surprise find of *Dryopteris submontana* (Fraser-Jenkins and Jermy) Fraser-Jenkins on the north side of Geyik Dağı, new to Turkey (see Parris and Fraser-Jenkins 1980), and otherwise known from Europe, reaching its nearest point to Turkey at Mt. Parnassos in Greece. It is also known from the western Caucasus in Abkhazia, U.S.S.R., where the first-named author has been fortunate enough to see it in 1976; it was long known erroneously under the name *D. villarii* (Bell.) Woyнар ex Schinz et Thell., as in Britain, before the taxonomy of the group was worked out (Fraser-Jenkins 1977). The Turkish plants appeared to be slightly different from most of the European ones in their more adnate, less lobed pinnules with very long teeth at their apices (though similar plants also occur in Crna Gora (Montenegro), Yugoslavia, as, for example at the Čakor Pass, west of Peć), but they are clearly within the range of *D. submontana* and have the characteristic dense, sticky-glandularity of that species. A chromosome-count carried out by the second-named author on the plant from Geyik Dağı (CRFJ 9809, BM) has confirmed that it is tetraploid ($n = 82$), which, along with its morphology, demonstrates its distinctness from the other two species in the erstwhile *D. villarii* cytological complex, *D. villarii* and *D. pallida* (Bory) C. Chr. ex Maire et Petitm., which are both diploid. Recently the first-named author has also seen a further, previously unidentified, specimen of *D. submontana* from the Ala Dağları (Nigde province), coll.: Findlay 227 (E), and it could therefore also be expected elsewhere in the Taurus, including the Bey Dağları in the western Taurus. The

remoteness and lack of road access to many of the mountains in the Taurus range probably explains why it has not been found before and suggests the strong possibility of the existence there of other interesting and overlooked species of ferns.



FIGURE 1.
Holotype of *Asplenium tadei*

COLLECTION OF THE NEW SPECIES

On 9th September 1979 a first attempt was made to find the *Asplenium*, setting off by car well before dawn from a motel at Manavgat on the coast. The narrow and rough route to Geyik Dağ turns off the main road north from Manavgat to Konya to head eastwards to the village of Gündoğmus, in the foothills of the mountains. In roadside limestone crevices in the *Pinus brutia* Ten. forest there occurred at c. 750m alt. numerous populations of *Dryopteris pallida* subsp. *libanotica* (Ros.) Nardi, a diploid taxon very close to subsp. *pallida*, differing only in having distinctively marginal sori with a wide gap between the two rows of sori on each pinnule. Interestingly, in this area of Turkey there is a transition between subsp. *pallida* in the west and subsp. *libanotica* in the east (and Cyprus, the Lebanon etc.), and the populations here contained some clearly transitional forms (with good spores, not hybrids) as well as both subspecies. Beyond Gündoğmus the forestry road turns northward into the main range and becomes even more narrow, rough and tortuous, being used mainly by small trucks sadly carrying away quantities of the natural forest as timber, and passing along spectacular cliff-edges above the forest, winding up into extremely rugged, higher-level open limestone crags, where it passes the shepherds' village of Güzelbag

and comes out, some four hours (by Range Rover) after the start, at the base of the peak of Geyik Dağı itself. On this first visit a direct and very hot and tiring ascent was made up the steep and dry west side of the mountain, over a ridge to the north-facing cirque, still containing snow-patches which last all through the summer, below the summit arête. At c. 2300m alt. plentiful *Cystopteris alpina* (Lam.) Desv. [= *C. regia* auct., non (L.) Desv.; lectotype in herb. Hort. Cliff. (BM!) is *C. fragilis*, (L.) Bernh., not *Asplenium foreziense* Le Grand as stated by Fuchs (1956 and 1980)], with its very finely dissected fronds, was found, along with a hybrid, probably *C. alpina* × *C. fragilis* and also occasional *Asplenium lepidum* Presl. subsp. *haussknechtii* (Godot and Reuter) Brownsey, a species somewhat similar to *A. ruta-muraria* L.; but disappointingly there was no trace of the species being searched for. A second ascent was made on 12th September 1979 from the north side of the mountain after following a driveable shepherds' track around the base. Above some shepherds' huts at 2250m alt. a population of the correct *Asplenium* containing about 20 plants was discovered, with great delight, growing in crevices on some north-facing limestone cliffs. Unfortunately further investigation into the size and altitudinal extent of the population and into the presence of other species or hybrids suddenly became a great deal less interesting a proposition, and indeed was somewhat hastily abandoned due to the appearance of a gun-toting young man of somewhat wild appearance and ambiguous intentions, armed, as he demonstrated, with a fully loaded Czech pistol, and who, while waving his pistol in their direction, insisted on accompanying the collectors down the mountain in a state of slightly awkward tension to where the car was parked below. There, fortunately, traditional Muslim politeness was just able to be maintained, with a few expressions of Turkish, and it was possible to turn the car and depart somewhat speedily around the side of the mountain and back on to the road-track. In all, five specimens of the *Asplenium* were collected and pressed (CRFJ 9812-9816) and an offset of CRFJ 9812 was transported living, partly wrapped in moss, to Basel to be grown by Professor Reichstein. It was immediately obvious in the field that this species did not closely match any other, including *A. daghestanicum*; it appeared in morphology most like *A. viride*, but with more deeply lobed lower pinnae and the distinctive fused frond-apex mentioned above. Although difficult to grow, including from fresh spores, the plant lived long enough in culture at Basel for a fixing to be made by Professor Reichstein and sent to the second-named author, who in August 1981, obtained a tetraploid chromosome count on it, with $n = 72$, at meiosis. In our opinion the collection clearly represents a new species, and we describe it, named in honour of Professor Tadeus Reichstein, thus:—

DESCRIPTION

***Asplenium tadei* Fraser-Jenkins et Schneller, sp. nov.**

Planta morphologia similis ad *A. viride* sed pinnis profundiore lobatis et pinnatifidis-tripartitis earibus differt. Apex frondis insignis segmentum lanceolatum constantum ex aliquot paribus connatis pinnarum est et aliquot lobi angusti ad margines fert. Cytotypus tetraploideus sexualis.

Holotypus: Turkey: "*Asplenium tadei*, sp. nov. Holotype. N. side of Geyik Dag, above shepherds' huts, N. of Gündogmus, N. of Alanya, Antalya Vilhayet, Turkey. N. facing shaded limestone cliffs, 2250m alt. C.R. Fraser-Jenkins (9815) and S.J. de C. Coombs, 12/9/1979" (BM!) (Fig. 1).

Isotypi: ditto (BM! Herb. T. Reichstein (5124 c), Basel!). Paratypi: ditto 9812 (BAKU! CANV! BM! Herb. T. Reichstein (5123 A), Basel!), 9813 (G! Herb. T. Reichstein (5124 A), Basel!), 9814 (K! P! PE! Herb. T. Reichstein (5124 B), Basel!) and 9816 (BM! Herb. T. Reichstein (5124 D), Basel!). Plant similar in morphology to *A. viride* but differing in its pinnae being more deeply lobed, with narrow extended lobes, and becoming pinnatifid-trilobate near the base of the lamina. Sori crowded near the base and centre of each pinna. The distinctive frond-apex is a lanceolate segment consisting of several fused pairs of pinnae and bears

several (c. 5-7) pairs of narrow lobes at the sides. Stipe often as long as the lamina, green, with a brown base extending up to $\frac{1}{3}$ of its length; bearing minute filiform, dark scales at its base which become smaller but are scattered up the whole length of the stipe. Cytotype tetraploid sexual (CRFJ 9812, det. J.J. Schneller; T. Reichstein, *pers. comm.* 18 August 1981).

ORIGIN AND RELATIONSHIPS

As *Asplenium tadei* is a tetraploid species whose morphology does not fit any known diploid species it seems likely that it may be an allotetraploid (amphidiploid) species along with the great majority of other European and western Asian tetraploid species, and indeed the concept of a mixed morphology can probably explain most of the appearance of the species. From the narrowness of the frond, the undivided pinnae and mostly green stipe and rhachis it seems likely that *A. viride*, with which it grows sympatrically on Geyik Dağ, could very probably be one of its ancestral diploid species. The other ancestor is less clear, though it must be a species with more lobed and probably longer pinnae. As no other diploid species occur today in the European (*sens. lat.*) flora which have a fused frond apex similar to *A. tadei*, it is impossible to do more at this stage than make a vague guess as to the rest of its origin, and it should be borne in mind that there exist two groups of mainly Asian species, the *A. exiguum* and *A. daghestanicum* aggregates which all have such a feature, so that *A. tadei* may well belong to one of these groups as a markedly distinctive member, with a diploid ancestor in one of the groups, possibly shared with *A. daghestanicum*. There is also a possibility that its second ancestor could be the south Turkish, Lebanese and Greek Aegean islands (Rhodes, Kastellorizo and Karpathos) endemic *A. bourgaei*, another species present in the vicinity (see Greuter *et al.* 1983), but at much lower altitudes (up to c. 900m) nearer the coast. *A. bourgaei* has longer, narrower pinnae bearing lobes which are widely joined at their bases; it also has a tendency for the bases of the upper pinnae to fuse together near the frond apex, but not nearly as markedly or widely as in *A. tadei*. However, in an allopolyploid combination it is often difficult to predict which characteristics will be emphasised and which not. Greuter *et al.* (1983) mentioned Davis' record of his specimen (which they did not see) under *A. bourgaei*, but stated correctly that because of its "completely aberrant" altitude it needed confirmation and might be due to some confusion. *A. bourgaei* has not so far been treated as in any way close to *A. exiguum*, but we believe that both it and the rare and restricted south French endemic, *A. jahandiezii* (Litard.) Rouy are closer to the *A. exiguum* group (including the Sino-himalayan *A. nesii* Christ) than to any other European species, though on a larger, world-wide scale, such groups may not be so clearly applicable.

Further study of *A. tadei* including attempted hybridisation work will be carried out by Professor Reichstein at Basel.

ACKNOWLEDGEMENTS

The authors wish to thank Professor Reichstein for his help in studying this species, and the first-named author is most grateful for his kind financial grant in aid of his expedition to collect it. They also wish to congratulate him on the achievement of his 90th birthday.

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THE FERN HERBARIUM OF COL. F.J. HUTCHISON

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ABSTRACT

The history and composition of F.J. Hutchison's fern herbarium is given, based on a manuscript catalogue prepared by H. Stansfield, and extracts are quoted from relevant correspondence. The herbarium contains material from 24 collectors, including Edwin Atkinson, Lady Anne Barkly, Francis Brent, John Buchanan, Charles B. Clarke, John Day, Wilhelm Hillebrand, George F. Hose (Bishop of Singapore & Sarawak), F.J. Hutchison and his probable relative H. McLeod Hutchison, Phoebe Moss, Charles Parish, Thomas Powell, Richard Spruce, William Stout and George Wall. Hutchison's own collections were largely made between 1870 and 1872 in Ceylon (Sri Lanka); they came to Liverpool Museum via the Royal Albert Memorial Museum, Exeter.

HISTORY OF THE COLLECTION

One of the largest collections of tropical ferns in the herbarium of Liverpool Museum (LIV) was presented in 1947 by the Royal Albert Memorial Museum, Exeter. It had been acquired from the widow of Col. Frederick J. Hutchison, shortly after his death on December 2, 1981 at Stoke, Devonport, Devon. The collection amounts to some 1,800 mounted sheets, and is noteworthy because it is composed not only of material collected by Hutchison himself in Ceylon, but also of exchange herbarium material sent by some well-known pteridologists of the mid-Victorian period.

Three categories of material can be recognised. Firstly, there are specimens which Hutchison himself collected between 1870 and 1872 in Ceylon (and a few from Dartmoor and Bovisands (1875), Perthshire (1876) and Ascot (1879). The total number comes to 310 sheets. The principal collection localities in Ceylon are given in Table 1.

Secondly, specimens acquired by Hutchison from his pteridological contacts amount to some 1553 sheets. A list of these collectors is given below. Both categories consist of material mounted on "fern-size" sheets (21 x 13 inches), are fully catalogued and numbered in taxonomic sequence from 1 to 1,863.

Lastly, there is a large and bulky series of unmounted material, much of which is only skimpily labelled. Some may duplicate Hutchison's collections. The number of unmounted and uncatalogued specimens was estimated at 9,000; this figure should be treated with caution, as some of the material consists of sequences of dismembered frond segments stored in separate paper folders which could be reassembled into a single frond.

The catalogue of the mounted material in the Hutchison fern herbarium was prepared by the Museum's former Keeper of Botany, Mr H. Stansfield, and was completed in 1958. No attempt was made to revise the nomenclature, which retains the taxonomic treatment adopted by Hutchison. This adheres closely to *Synopsis Filicum* (Hooker & Baker, 1974). Many of the statistical data in this article have been extracted from Stansfield's catalogue.

TABLE 1.
Gazetteer of collection localities in Ceylon (Sri Lanka) visited by F.J. Hutchison
(Spelling as on labels)

Aggelwatte	10.1871	Galagana	4.1872
Bullatotte Pass	7.1871	Galle	7.1871
Colombo	8-9.1870, 7.1871, 9.1871	Gonaganna	2.1872
Condagalle Pass	1.1871	Gongolla	4.1872
Dimboola Pass	3.1871	Hakgalla	1-2.1871, 5.1871

Hantam	1.1871	Newera Eriya	1-2.1871
Hapootella	5.1871	Oodoowelle	10.1870, 1.1871
Helbodde	8.1870	Pittawelle	8.1871
Hewissa	10.1871	Poorie	5.1872
Hoolakande Pass	8.1871	Puselawe	8.1870, 1.1871
Horton Plains	4.1872	Rambodde Pass	1.1871
Kambodde	8.1870, 1-2.1871	Rambodde	2.1871
Kandy	10.1870	Rottowa forest	7.1871
Kegalli	6.1872	Telgamma	10.1871
Kornegalle	2.1870	Vicarton	8.1871
Maturalta	4.1871	West Matala	8.1871
Morowa Korle	7.1871		

HUTCHISON'S FELLOW ENTHUSIASTS

Although Hutchison's own collecting activities in Ceylon were carried out privately while he was stationed there (with the rank of Major), it is clear from correspondence held at Liverpool Museum that he collaborated closely with the principal pteridologists of the period in Ceylon. One of these was Thomas W. Naylor Beckett (1839-1906), a coffee planter, whose herbarium and correspondence is kept at Liverpool Museum. Naylor Beckett was born in Liverpool and spent much of his life in Ceylon before moving to New Zealand in 1883.

A letter addressed to Naylor Beckett from George Wall, a fern enthusiast resident in Ceylon, describes a recently completed fern-hunting expedition. Dated "Colombo, July 23, 1871", it commences:

"My dear Sir,

I returned here last night from a trip through Moosoowakka Suffragum & Rahnapoora with Major Hutchison. I went on business but took my fern papers and worked on the way. Your kind letter and most valuable catalogue awaited my return and I lose no time in thanking you for them.

We had awful weather, but except on one day we carried out our programme and worked through the dreadful downpour, regardless of leeches and all the multiform discomforts of incipient rain. — I think we have made a very good bag, all things considered, and we have confirmed an opinion which we have both gradually been brought to that even the rare ferns are much more widely spread than generally supposed. Your list is in itself a strong confirmation of that opinion too ..."

The letter continues with a list of the chief new finds. It was written on a date midway through Hutchison's period of fieldwork; see Table 1.

Included in the correspondence on file in Liverpool is a letter to Beckett from F.J. Hutchison dated "Columbo, 30 Dec. '71". It reads, in part:

"... Mr Wall wrote to you a full account of our doings at Matala, and I hope expressed, as I asked him to, my acknowledgments to you, with his own, for the excellent instructions you have given us, thanks to which the expedition was the most successful we had ever made ... We had, as you know, planned two other expeditions, one to your part of the country and another to the Singh Raja Forest, both of which Mr Wall's engagements forced him to give up, much to our disappointment. The latter I have since partially accomplished, partially only, because I found the distances were not at all what I had been led to expect. In fact to quote Mr Thwaites, to whom I sent an account of my doings, I got "the cream of the Singh Raja Forest ferns."

Mr Wall has written to me thrice since he reached England. He has had some interviews with Baker at Kew [1], and sent me a copy of notes made there on some of the Ceylon ferns which I will enclose as I have no doubt you will be interested in them. You will see that Baker pronounces the *Acrostichum*, which we found near Morawaka, and of which Mr Wall sent you a specimen, to be a distinct species [2] and not merely a form of *A. (Gymnopteris) variabile* as we supposed ...

There will not I fancy be many gaps in your Ceylon collection but it is possible that I may be able to fill some of them for you, and I need scarcely say that it will give me the greatest pleasure to do so ..."

Notes: [1] John Gilbert Baker (1834-1920) was then an Assistant Curator of the Kew herbarium; later (1890-1899) he held the position of Keeper.

[2] Possibly a reference to *Acrostichum wallii* Baker, ascribed in the Appendix to Hooker & Baker (1874), p. 523.

There is also at Liverpool a letter to Beckett from Wall dated "Colombo, 19 July 1872" which refers to "Major H.". The text of the letter is as follows:

"My dear Sir,

I acknowledged your kind letter a day or two ago and I now send you a list of the ferns I have yet to find. It is cleared of several by my last trip and does not contain a large proportion of very rare ones. Of these I have been fortunate in finding a good many. Of *Diacalpe Aspidioides* for instance Major H. and I discovered the headquarters between Mathooratee [1] and Ordupusselmon on the Kooroonda Oga where we found it in profusion and of great size. One frond I gave Mr Thwaites [2] was 2 feet long without the stipes. — Still I have a deal to do to complete my collection of known ferns, especially as some of those I found at first I spoiled not knowing how to manage them. I have not more than 150 or 160 species mounted and fit to mount.

I have also suffered loss by insects, and it is a serious labour to poison all even with my rolling apparatus, which is infinitely more expeditious than the feather or brush. I hear there is a better method of poisoning by means of the fumes of Carbolic Acid. — Do you know this method?

I fear I shall not be able to visit Dick [3] or you again so soon as I intended: but I must go to East Matali and to Singhe Rajah forest before I go home if possible -

The *Nephrodieae* trouble me so much and I do not take much notice of them, as I expect to tackle them separately when I have cleared off all the rest. Latterly I have collected considerable quantities of all the ferns I have found, so I hope to be able to requite your kindness by contributing to your collection. I send herein a frond of an *Acrostichum* which I suppose I am bound to call *Ac. Variable* [4] but my series of this plant was already most remarkable before I added this to the strange variety of forms this fern assumes. Do you know this form?

More anon

Yrs very Sincerely,
George Wall."

Notes: [1] Hutchison has a specimen of *Diacalpe aspidioides* (cat. no. 103) from "Maturatte, April 71". This species is now sometimes known as *Peranema aspidioides* (Blume) Mett. (e.g. Sledge, 1982).

[2] G.H.W. Thwaites (1812-1882) was, at the time, Director of the Botanic Gardens at Peradeniya, Ceylon. According to Desmond (1977), G. Wall was a friend of his.

[3] "Dick" is possibly a reference to Richard Henry Beddome (1839-1911), author of "Ferns of British India" (1865-70).

[4] Now known as *Leptochilus decurrens* Blume.

The Hutchison herbarium contains 42 specimens contributed by George Wall in addition to those which were collected during joint excursions. It is significant, however, that Hutchison did *not* receive material from either Thwaites or Naylor Beckett.

The list of collectors represented in the Hutchison herbarium includes only one other botanist resident in Ceylon: William Ferguson (1820-1887), a civil servant in Ceylon who published various works including "Ceylon Ferns" (1872) and "Ceylon Ferns and their Allies" (1880). There are letters from Ferguson to Naylor Beckett in the files at Liverpool, one of which reveals that Beckett assisted Ferguson in the editing of his "Ceylon Ferns" prior to publication.

The picture one builds up is of a group of enthusiasts co-operating in the mutual enrichment of their collections, some of whom — Hutchison included — were able, through fieldwork, to contribute rarities at the request of other collectors and who in turn acquired valuable exsiccata from other parts of the world.

INDEX OF COLLECTORS

It is unclear how Hutchison obtained material from collectors of non-Ceylon material and if information comes to light the Liverpool Museum would be grateful to receive it. The following collectors are the principal outside contributors to the Hutchison herbarium (numbers of specimens are given in square brackets):

Atkinson, Edwin (1840-1890). Entomologist, Indian Civil Service, 1862-1890. Sikkim, Khasya Hills, East Indies. [50]

Barkly, Lady Anne Maria (1838-1922). Second wife of Sir H. Barkly (1815-1898). Reunion, Mauritius, Namaqualand (Namibia, S.W. Africa). [44]

Boyd, Miss. Dates and occupation unknown. Sandwich Is. (Hawaii). [15]

Brent, Francis (1816-1903). H.M. Customs officer; the specimens are from Brazil, though it is unlikely that Brent collected them himself. There are no references to Brent, nor to Randall (q.v.) as collectors in Martius & Eichler, *Flora Brasiliensis*

- vol. 1, 1906: chapter entitled "Vitae Itineraque Collectorum Botanicorum"
See also Greenwood (1972). [16]
- Buchanan, Revd. John.** Minister, Durban, South Africa, 1861-1874. [211]
Orange River Colony, South Africa.
- Clarke, Charles Baron** (1832-1906). Superintendent of Calcutta Botanic Gardens, 1869-71; worked at Kew after retirement. Co-author (with Henderson) of "Ferns of N. India" (1880). Dhurmsala, India, 1874. [1]
- Corrie, Dr.** Dates and occupation unknown. Fiji. [few]
- Craig, ?William** (fl. 1880-1890), an Auckland dealer in fern exsiccata. Provenance given as "New Caledonia". Although only a few specimens are attributed to "Craig" in Stansfield's catalogue, there is a significant number of specimens from New Caledonia which lack details of the collector. By checking the names of such ferns in *Flore de la Nouvelle Calédonie*, no. 3: *Ptéridophytes* (Brownlie, 1969) it is clear that they include a number of endemic species collected by Vieillard. It is likely, though difficult to prove, that Craig supplied Hutchison with a collection whose labels had been lost or discarded.
- Day, John** (1824-1888). Amateur fern and orchid enthusiast and traveller. Australia, Ceylon, Fiji, Indonesia, Japan, New Zealand, West Indies (Trinidad, Jamaica). Most are from Japan. [252]
- Ferguson, William** (1820-1887). Surveyor, Ceylon Civil Service. Author of "Ceylon Ferns". Ceylon, St. Helena. [3]
- Gamble, James Sykes** (1847-1925). Employed in the Indian Forest Service from 1871, and Director of the Forestry School at Dehra Dun from 1890-99. Sikkim, 1872. [2]
- Grant, James Augustus** (1827-1892). Army Officer. Hong Kong. [1]
- Gray, Samuel O.** (1828-1902). Author of "British Seaweeds" (1867). West Indies (St. Vincent). [2]
- Hillebrand, Wilhelm** (1821-1886). German doctor and botanist, resident in Hawaii 1851-1871. Author of "Flora of the Hawaiian Islands" (1888). Java, Samoa, Sandwich Islands (Hawaii). [114]
- Hose, Revd. George Frederick** (1838-1922). Bishop of Singapore and Sarawak, 1881-1908. Malaya, Sarawak. [83]
- Hutchison, H. McLeod** (1840-1925). Army Officer. Probably a relative of F.J. Hutchison, but exact relationship unknown. According to Hart's Army List for 1867, he was Lieut. in the 14th (Buckinghamshire) Regiment of Foot, whose 2nd Battalion returned from Jamaica in 1864. Jamaica (see also Prior). [119]
- Moss, Miss Phoebe** (dates unknown). An amateur naturalist who, in 1885, introduced the Common Myna (*Acridotheres tristis*) and the Grass Frog (*Rana grayi grayi*) to St. Helena. [Information from Dr Q. Cronk in litt. 24.11.1982]. St. Helena, South Atlantic Ocean. [11]
- Munroe, W.** (1818-1880). Army Officer and agrostologist; General, 1878-1880). Canada (Quebec), 1859. [2]
- Parish, Revd. Charles S.P.** (1822-1897). Army Chaplain. Burma (Moulmein). [42]
- Powell, Revd. Thomas** (1809-1887). Missionary in Samoa, 1860-85. Samoa. [29]
- Prior, Richard C.A.** (1809-1902). Curator of Fielding Herbarium, Oxford. Jamaica. Many Jamaican specimens lack details of the collector; they may have been collected by either H. McL. Hutchison or Prior.
- Randall, Mr.** Dates unknown. Brazil. See note under Brent. [20]
- Spruce, Richard** (1817-1893). One of the most notable botanical explorers of South America. Mainly Peru. [11]
- Stout, William** (d. 1882). U.S.A. According to Joseph Ewan, this is one of the largest collections of Stout's material. [152]
- Wall, George** (c. 1821-1894). Head of the firm of George Wall & Co., a businessman based in Colombo and keen amateur pteridologist. Ceylon. [42]

ACKNOWLEDGEMENT

I am indebted to Stephen Harrison for his unpublished notes on the Hutchison herbarium, which saved me much time in the preparation of this account.

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THE STATUS OF *OPHIOGLOSSUM AZORICUM* (OPHIOGLOSSACEAE : PTERIDOPHYTA) IN THE BRITISH ISLES

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ABSTRACT

The status of *Ophioglossum azoricum* in the British Isles is examined by comparing the gross morphology, epidermal features, spores and cytology of the three British species of *Ophioglossum*, *O. azoricum*, *O. lusitanicum* and *O. vulgatum*, together with their ecology and distribution. The possibility that *O. azoricum* is just an ecotype of *O. vulgatum* is considered. It is concluded that these two taxa cannot be satisfactorily separated morphologically and that *O. azoricum* appears to be merely at one end of the spectrum of variation shown by *O. vulgatum*. *O. azoricum* is maintained as a separate species for the present because certain populations are so distinct in habit, but it is now evident that cytological investigation combined with extensive field studies is necessary to elucidate the status of this taxon.

INTRODUCTION

The taxon now known as *Ophioglossum azoricum* C. Presl was first found and recognised in Britain as distinct by J. Boswell Syme in the Orkneys in the mid-19th century (Boswell Syme 1871). Due to its similarity to *O. vulgatum* L., it has been referred to as a variety or subspecies of that species in the European literature for well over 100 years. However, in 1964, Rothmaler accepted *O. azoricum* as a species. He described it as morphologically distinct from *O. vulgatum*, and intermediate in many respects between that species and *O. lusitanicum* L.

The nomenclature of the taxon has been rather confused (see synonymy below). This can be principally attributed to the existence in Africa and parts of western Asia of a further taxon, *O. polyphyllum* A. Braun, which was erroneously regarded by some botanists as a subspecies or variety of *O. vulgatum*, and to which some European specimens were referred. Pichi-Sermolli (1954) showed that *O. polyphyllum* was distinct from the European plants, which he referred to *O. vulgatum* var. *ambiguum* Coss. & Germ. A comparison of these two taxa and their distribution in Macaronesia is given by Lobin (1986).

There are three species of *Ophioglossum* in the British Isles, of which one, *O. lusitanicum*, may easily be distinguished morphologically from the other two. Its winter growing season also means its identity is unlikely to be mistaken. *O. azoricum* and *O. vulgatum*, however, are less easy to separate, as most of their characters overlap markedly in range. This comparative study of the three taxa was undertaken to find characters to distinguish the two summer-growing species, and also to see if *O. azoricum* is truly intermediate between the other two and sufficiently distinct to warrant specific recognition.

Synonymy

Ophioglossum azoricum C. B. Presl. 1845. Suppl. Tent. Pterid.: 49.

O. vulgatum subsp. *polyphyllum* E.F. Warburg. 1952. in Clapham, A.R., T.G. Tutin & E.F. Warburg, Fl. Brit. Is.: 54. pro parte excl. syn. A. Br.

O. vulgatum subsp. *ambiguum* (Coss. & Germ.) E.F. Warburg. 1957. Watsonia. 4: 41.

O. vulgatum var. vel subsp. *polyphyllum* auct.; non *O. polyphyllum* A. Braun in Seubert, 1844. Fl. Azor.: 17. (vide Pichi-Sermolli 1954).

CYTOLOGY

Löve and Kapoor (1966, 1967) suggest that *O. azoricum* is of hybrid origin, an allopolyploid derivative of a chance hybrid between *O. vulgatum* and *O. lusitanicum*. The taxon may be intermediate morphologically, but the cytological basis for their hypothesis is founded on insubstantial evidence.

Few chromosome counts have been reported for European specimens of *Ophioglossum*. These are summarised in Table 1. As yet, counts for British plants have been published from only one sample each of *O. lusitanicum* and *O. vulgatum* (Manton 1950) and none for *O. azoricum*. European counts suggest the chromosome number of *O. vulgatum* is $n = 240-260$, and of *O. lusitanicum* is $n = 125-130$. However, Löve and Kapoor (1966, 1967) give the chromosome number of *O. lusitanicum* as $2n = 240$, but with no reference source. Furthermore, their count for *O. azoricum* ($2n = 720$) is based only on Icelandic material. They consider their earlier count (given under the name *O. vulgatum* ssp. *ambiguum* var. *islandicum* Löve & Löve, in Löve & Löve 1961) of $2n = 480$ to be an inexact estimate. This is presumably the basis of ' $2n = c.480$ ' cited for *O. azoricum* in *Flora Europaea*; Rothmaler's decision to recognise the taxon here as a good species was not based on cytological evidence.

Further cytological studies of this genus in Britain and Europe as a whole (including the Azores) are obviously required, particularly to help establish the status of *O. azoricum*. It is interesting to note that Japanese material of *O. vulgatum* has also given a chromosome count of $n = 240$ (Kurita & Nishida 1965), but that Indian specimens of *O. lusitanicum* and *O. vulgatum* have revealed chromosome numbers of a range approximately double those of European and Japanese material (Ninan 1956, 1958, Verma 1956).

TABLE 1. European *Ophioglossum* chromosome counts

Species	Origin	Author & Date	n	2n
<i>O. lusitanicum</i>	Guernsey	Manton 1950	125-130	c. 344*
<i>O. vulgatum</i>	England	Manton 1950	c. 128	
<i>O. vulgatum</i>	Sweden	Ehrenberg 1945	250-260	
<i>O. vulgatum</i>	Netherlands	Verma 1958	c. 256	
<i>O. vulgatum</i>	Finland	Sorsa 1962	240, 247-	c. 480
<i>O. vulgatum</i>	Spain	Löve & Kjellqvist 1972	251 (c. 248)	
<i>O. vulgatum</i>	Sweden	Löve & Löve in Löve 1976	c. 250	
<i>O. azoricum</i> **	Iceland	Löve & Löve 1961		
<i>O. azoricum</i>	Iceland	Löve & Kapoor 1966, 1967		480
		Löve & Löve in Löve 1976	360	720
				720

* based on sectioned cells rather than a 'squash'
** as *O. vulgatum* subsp. *ambiguum* var. *islandicum*

MORPHOLOGY

General morphology

As previously mentioned, *O. lusitanicum* is morphologically distinct from the other two British species, but *O. azoricum* and *O. vulgatum* overlap considerably in their range for most characters. They are usually separated by the number of fronds per plant,



FIGURE 1. a, *Ophioglossum vulgatum*, Morfa Dyffryn, Merioneth. x1. (photo. A. Cleave). b, *O. lusitanicum*, St. Agnes, Scilly Isles. x2. (photo. K.H. Hyatt). c, *O. azoricum*, Ravensglass, Cumberland. x2. (photo. A.C. Jermy). d, *O. azoricum*, S. Uist, Outer Hebrides. x2. (photo. A. Cleave).

frond size and shape, and the number of sporangia per fertile spike. For example, two of the criteria used to recognise *O. azoricum* for the *Atlas of Ferns of the British Isles* (ed. A.C. Jermy *et al.* 1978) were 14 or less pairs of sporangia and a sterile blade less than 3.5cm long.

O. vulgatum is said to produce usually only one frond, occasionally two per plant, whilst *O. azoricum* and *O. lusitanicum* regularly bear 2-3 fronds. However, populations observed in the field or preserved as herbarium specimens indicate that *O. vulgatum* produces more than one frond more commonly than is generally supposed, and the other species have usually two fronds, sometimes one, and occasionally three.

O. lusitanicum is not a variable species. Sterile blades are narrowly lanceolate, 8-23(-38)mm long, 1.5-4(-6)mm wide. They are widest at about the centre of the frond, narrowing gradually to the base and apex, the latter being slightly rounded. The sterile blades of *O. vulgatum* tend to be broadly ovate-lanceolate to ovate, usually widest below the middle. They are extremely variable in size and shape even within a single population, 17-150 x 8-58mm, with the apex ranging from acute to very rounded or apiculate. The base may be attenuate to cordate, often clasping the stem. Some specimens of *O. vulgatum*, on the other hand, are relatively small, with lanceolate sterile blades, and are very similar to those of *O. azoricum*. The latter have blades 9-22 (-40) x 4-10(-14)mm which are broadly lanceolate to ovate, usually with cuneate bases and acute to obtuse apices, the lamina being broadest at or just below the centre.

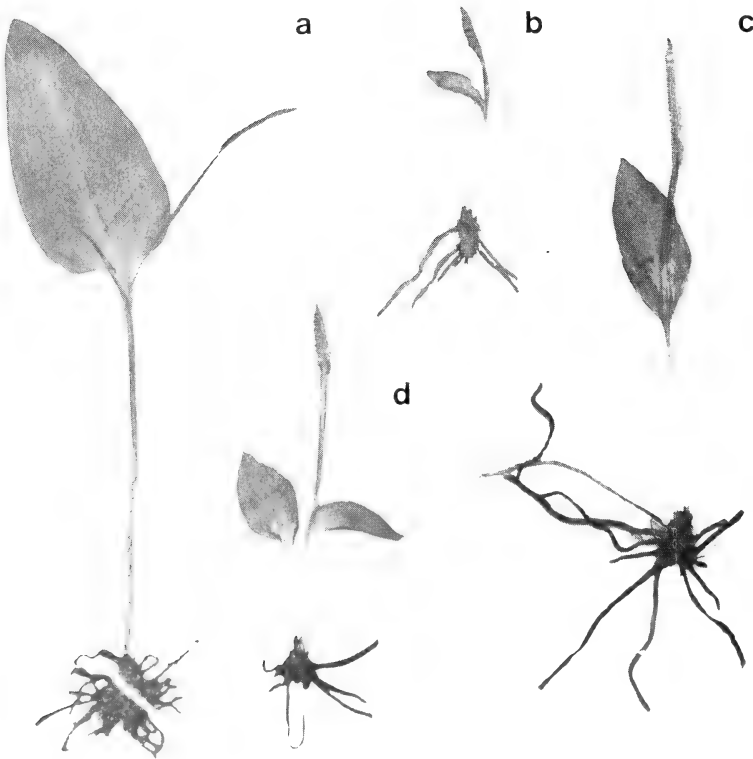


FIGURE 2. Herbarium specimens of *Ophioglossum*. a, *O. vulgatum*, R. Vowell Sherring, 1912, Enfield, Middlesex. x0.5. b, *O. lusitanicum*, M. Dawber, 7 January 1886, Guernsey, Channel Islands. x1. c, *O. vulgatum*, R.J. Pankhurst & A.O. Chater, 12 August 1983, Berneray, Outer Hebrides. x1. d, *O. azoricum*, A. Cleave, June 1983, S. Uist, Outer Hebrides. x1.

The angle at which the sterile blades grow is sometimes distinctive for different *Ophioglossum* species. Those of *O. lusitanicum* are often reflexed, and so held close to the ground (Fig. 1b), though occasionally they are more upright. Fronds of *O. vulgatum*, by contrast, tend to be quite erect (Fig. 1a). *O. azoricum* tends to resemble the former in its reflexed habit (Fig. 1c, d), a feature not mentioned in the type description, but shown by some individuals of the isotype (BM). This is, of course, a character which is often lost on herbarium specimens, however carefully they are pressed (Fig. 2), but it seems, generally speaking, to be one of the best field characters.

The other principal character commonly used is the number of pairs of sporangia on the fertile spike. *O. lusitanicum* has 3-8(-13), *O. vulgatum* 11-44, and *O. azoricum* 4-13(-17), the range for the latter overlapping that of the other two species. Size of fronds and sporangial number do not seem to be directly correlated; some specimens of *O. vulgatum* with tiny leaves (less than 2cm long) may have as many as 20 sporangial pairs, others far fewer, and likewise some large individuals have relatively few sporangia.

Other features of plants, such as the length of the fertile spike and the common stalk, and the relative proportions of fertile blades were studied for a large number of specimens, but did not prove to be useful in identification. They are very variable, differing with the maturity of the plant, depth of the rhizome below the soil surface, habitat and climate. The shape of the rhizome is also not constant. *O. lusitanicum* does tend to have an elongated, rather cylindrical rhizome, but in the other species small specimens have relatively small, globose rhizomes, whereas in larger individuals they are considerably bigger and much more elongated. Hand-cut sections of roots of varying sizes stained with safranin showed the stele of all three taxa to be monarch.

Venation and epidermal characters

Venation was one of the key characters on which Prantl (1884) based his classification of *Ophioglossum*. Clausen (1938), however, realised that venation was not a reliable character, due to its variability within a single population. In 1962, Mahabale based a key to Indian *Ophioglossum* species on characters of venation. Panigrahi and Dixit (1969) likewise considered venation important in identification, and Bhambie and Madan (1982) also reported venation patterns to be taxonomically significant at species level, in terms of areole number per unit area of frond. However, Wagner *et al.* (1981) and Wagner *et al.* (1984) showed that a single species could produce a range of fronds, from small ones with simple venation to large forms with more complex venation.

In this study, fronds taken from herbarium sheets were cleared in 10% bleach ('Domestos') and stained with an aqueous solution of methylene blue. They were thereafter stored in 50% alcohol. Venation patterns were drawn using a microscope drawing attachment, or by tracing photographs. *O. lusitanicum* was the most distinct species, having only a primary network of veins forming rather long, narrow areoles parallel with the mid-vein. Very few included free veinlets are present (Fig. 3a, b). The areoles of the primary vein reticulum of *O. azoricum* are less protracted, and the more central, larger areoles contain a finer secondary mesh. Included free veinlets are common but not numerous (Fig. 3c, d). The venation pattern of *O. vulgatum* is much more variable, probably owing to its range of frond size. In large fronds, the majority of primary areoles contain finer veins forming a secondary network, and also many free included veinlets (Fig. 3f). In smaller blades the secondary reticulum is less well-developed and has few free included veinlets (Fig. 3e), thus not being very significantly different to that of *O. azoricum*. Since it is usually small-fronded *O. vulgatum* specimens which tend to be confused with specimens of *O. azoricum*, it appears that

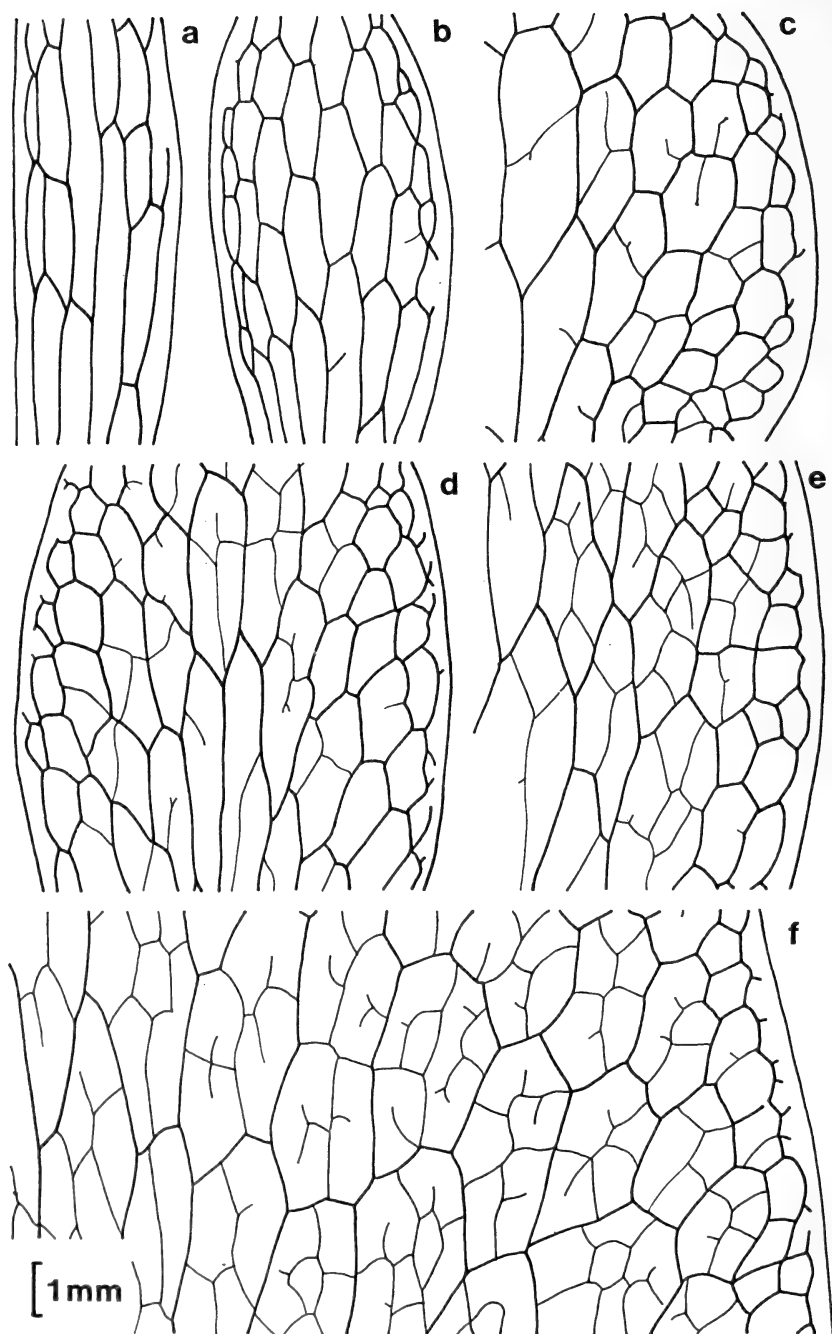


FIGURE 3. Venation of *Ophioglossum*. a, b, d, central portion across whole width of frond, c, e, f, central portion of frond from mid-vein to margin. a, *O. lusitanicum*, J.E. Gardner, Guernsey, Channel Islands. b, *O. lusitanicum* M. Dawber, 21 January 1886, Guernsey, Channel Islands. c, *O. azoricum*, A. Cleave, June 1982, Lundy, Devon. d, *O. azoricum*, J. Boswell Syme, August 1873, Swanbister, Orkney. e, *O. vulgatum*, R.J. Pankhurst & A.O. Chater, 12 August 1983, Berneray, Outer Hebrides. f, *O. vulgatum*, L.H.J. Williams 1053, 12 June 1935, Kemsing, Kent.

venation characters are of rather limited usefulness. If extensive studies of fronds of different sizes and developmental stages could be undertaken similar to those of Wagner *et al.* (1981), differences between the venation patterns of *O. azoricum* and small individuals of *O. vulgatum* might become evident. However, it is equally possible that *O. azoricum* would prove merely to be at one end of the spectrum of variation shown by *O. vulgatum*.

Epidermal characters, particularly cell-shape and stomatal orientation, have also been considered useful in distinguishing species of *Ophioglossum* (Prantl 1884, Mahabale 1962, Maroti 1965, Van Cotthem 1970, Pant & Khare 1969). For this investigation whole fronds, cleared and stained as above, were mounted and photographed using bright field microscopy. In one case the epidermis was peeled off and mounted in glycerine jelly. In each sample the area between the mid-vein and margin in the centre of the frond was photographed for comparative study and then drawn from the negative with the aid of a photographic enlarger.

Once again it is *O. lusitanicum* which is markedly different from the other species. The epidermal cells on the lower surface are narrowly rectangular and parallel with the long axis of the frond (Fig. 4b); on the upper surface the cells are squarer and more rounded (Fig. 4a). The lower epidermal cells of large fronds of *O. vulgatum* have very undulating margins, tending to be fairly long and narrow and parallel with the long axis of the frond (Fig. 4h); those of the upper surface have similarly undulating edges, but they are much more irregularly shaped (Fig. 4g). In small-fronded individuals, the epidermal cells of both surfaces are much smaller, with very much less sinuous margins (Fig. 4e, f). *O. azoricum* specimens studied greatly resemble small individuals of *O. vulgatum* in the shape of epidermal cells though the margins are rarely sinuous (Fig. 4c, d).

In all three species the stomata are sunken, and distributed more or less equally on both surfaces of the fronds. On the lower surfaces the stomata are all parallel with the main vein (Fig. 4b, d, f, h). In *O. lusitanicum*, the stomata on the upper surface are also mostly parallel with the long axis of the frond (Fig. 4a), but in the other two species they are randomly orientated (Fig. 4c, e, g), even in the centre of the frond.

Thus it seems that the epidermis does not provide good characters for separating *O. azoricum* and small specimens of *O. vulgatum*.

Spores

As early as 1857 spores were considered diagnostic for distinguishing European *Ophioglossum* species (Durieu de Maisonneuve 1857). Prantl (1884) placed considerable emphasis on spore size and ornamentation in his classification of the genus and these characters were also found to be useful in distinguishing Japanese species (Nakamura & Shibasaki 1959, Kurita 1981) and Indian species of *Ophioglossum* (Mahabale 1962, Pant & Khare 1971). However, in the most recent monograph of the genus, Clausen (1938) found spore characters to be of only limited value in distinguishing species, although this may in part reflect his broad species concept. Wieffering, in his preliminary revision of Indo-Pacific species of *Ophioglossum* (1964) implied that spores were characteristic only of sub-genera rather than species.

All spores used for this study were removed from herbarium specimens and were not chemically treated prior to observation. Spores were glued to stubs with 'Araldite', coated with gold palladium and examined with an Hitachi S800 SEM. Permanent preparations are kept at BM.

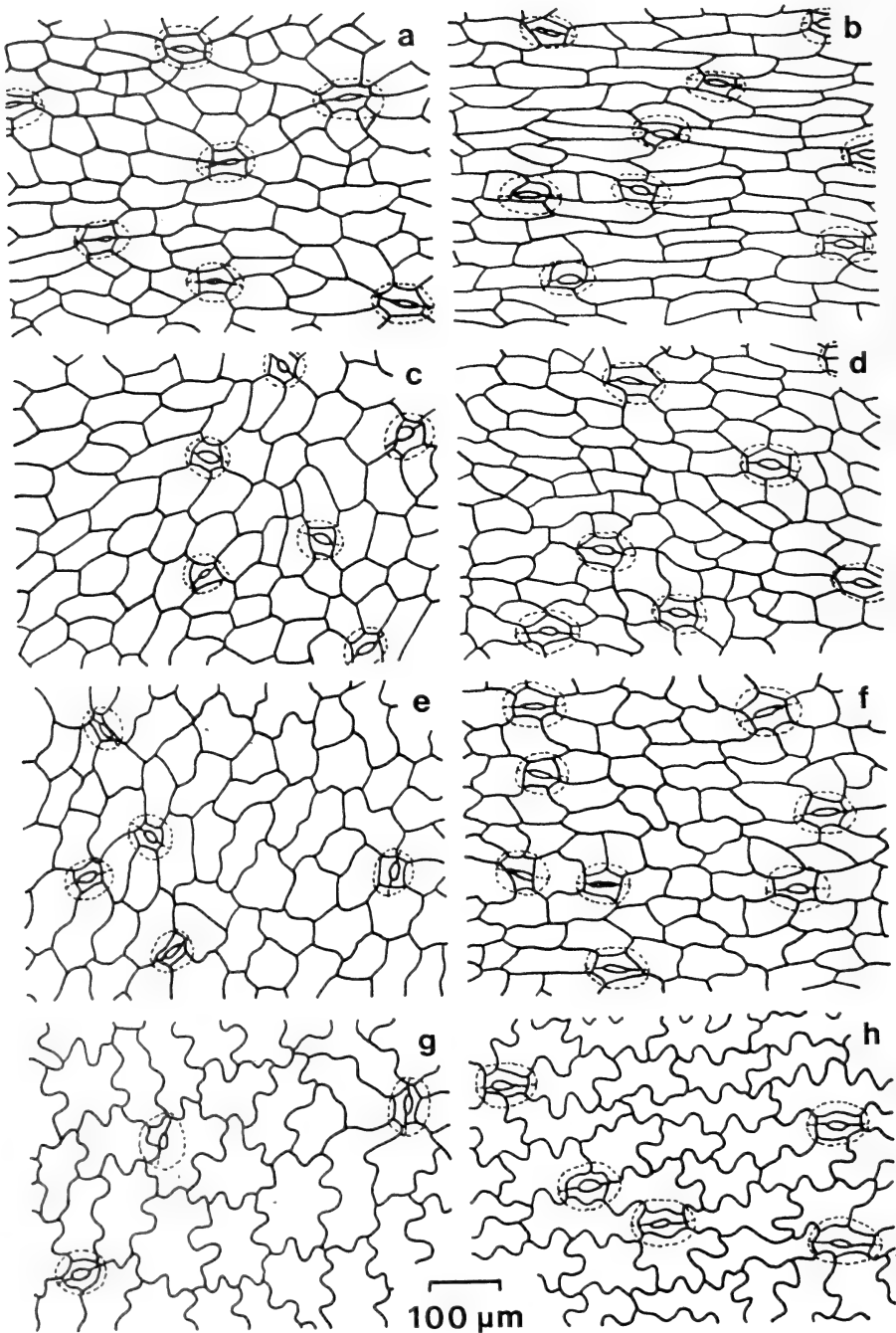


FIGURE 4. Epidermal features of *Ophioglossum*. Portion illustrated is from centre of sterile blade half-way between mid-vein and margin; vertical axis of frond is horizontal across page. a,b, *O. lusitanicum*, G. Wolsey, March 1869, Guernsey, Channel Islands; a, upper epidermis and b, lower epidermis. c,d, *O. azoricum*, A. Cleave, June 1982, Lundy, Devon; c, upper epidermis and d, lower epidermis. e,f, *O. vulgatum*, R.J. Pankhurst & A.O. Chater, 12 August 1983, Berneray, Outer Hebrides; e, upper epidermis and f, lower epidermis. g,h, *O. vulgatum*, F.J. Hanbury, 12 June 1875, Trotter's Cliff, Kent; g, upper epidermis and h, lower epidermis.

The equatorial diameter of spores, taken from at least five herbarium specimens of each species, was measured in air. The overall size range for 30 spores from each sample was as follows (range of sample means in bold):— *O. vulgatum* 28-**30-38**-43µm, *O. lusitanicum* 28-**29-34**-40µm, *O. azoricum* 35-**38-42**-45µm. Page (1982) also found that spores of *O. lusitanicum* tend to be smaller, and those of *O. azoricum* larger, than *O. vulgatum* spores, but Ferrarini et al. (1986) report spores of *O. lusitanicum* in Italy to be intermediate in size between those of *O. vulgatum* and *O. azoricum*. However, the ranges overlap considerably, and since a single sample may have a range of up to 10µm, it is important to use the mean size of a large sample. It should also be noted that the medium in which spores are measured has a bearing on size, and it is advisable to use controls of known identity.

Spore size is thus of limited usefulness, and the same seems to be true of the ornamentation of spores, as revealed by light microscopy (LM) and scanning electron microscopy (SEM). Spores of European *O. vulgatum* have been variously reported as being tuberculate (Durieu de Maisonneuve 1857, Rothmaler 1964), having small, but distinct blunt tubercles (Page 1982), lopho-reticulate (with projecting anastomosing ridges forming an open angular reticulum) (Harris 1955), having a coarse network, tubercular in outline (Verma 1958), verrucate, appearing reticulate (Pant & Misra 1976), reticulate with prominent lamellae (Knox 1951), reticulate with muri which vary remarkably in height and width (Ferrarini et al. 1986), and scabrose-foveolate or baculate (Moe 1974). *O. lusitanicum* spores, on the other hand, have been commonly described as smooth (Durieu de Maisonneuve 1857, Rothmaler 1964, Page 1982), though Knox (1951) described them as irregularly pitted, Fernandes & Queirós (1980) as finely reticulate with small areoles, Ferrarini et al. (1986) as foveolate, and Wildpret de la Torre et al. (1974) as granular. Spores of *O. azoricum* have been referred to as tuberculate (Rothmaler 1964), coarsely reticulate, not tuberculate (Bailey 1880) and reticulate-verrucate (Fernandes & Queirós 1980).

There is obviously a lack of uniformity of terminology throughout the literature, although there is considerable variation in spore wall ornamentation between spores of different populations of a species, and even of one individual. Spores of *O. lusitanicum* were more uniform than those of the other two species. SEM studies revealed *O. lusitanicum* spores were irregularly pitted with many small, irregularly shaped pits, these being more numerous on the distal surface (Fig. 5e, f). These pits are visible in LM, and the outline of spores in equatorial view appear almost smooth, but slightly crenate.

O. vulgatum spores are much more variable than those of *O. lusitanicum*. The majority of spores observed under SEM were deeply pitted, especially on the distal surface where the many large, irregularly shaped pits were crowded together, the pit walls thus forming a very irregular reticulum (Fig. 5b). On the proximal surface the pits are usually smaller and further apart (Fig. 5a). Some spores studied, however, have more widely-spaced pits, still forming a reticulum, but with some walls much wider and flat-topped. This supports the view that the reticulum comprises pit walls rather than tubercles. Under LM the equatorial outline of all spores is irregularly tuberculate, but the reticulum on the distal surface is also visible.

The spores of *O. azoricum* are generally intermediate in ornamentation between the above species. Most spores studied by SEM were irregularly pitted on both surfaces, the irregularly shaped pits being generally further apart on the proximal surface, and slightly larger than the pits of *O. lusitanicum* spores (Fig. 5c, d). LM observations also reveal these pits, and the equatorial view is not as smooth as in *O. lusitanicum* spores, but usually more regular and not as tuberculate as in spores of *O. vulgatum*. However, some *O. azoricum* spores have larger pits which are crowded together, forming a reticulum as in *O. vulgatum*.

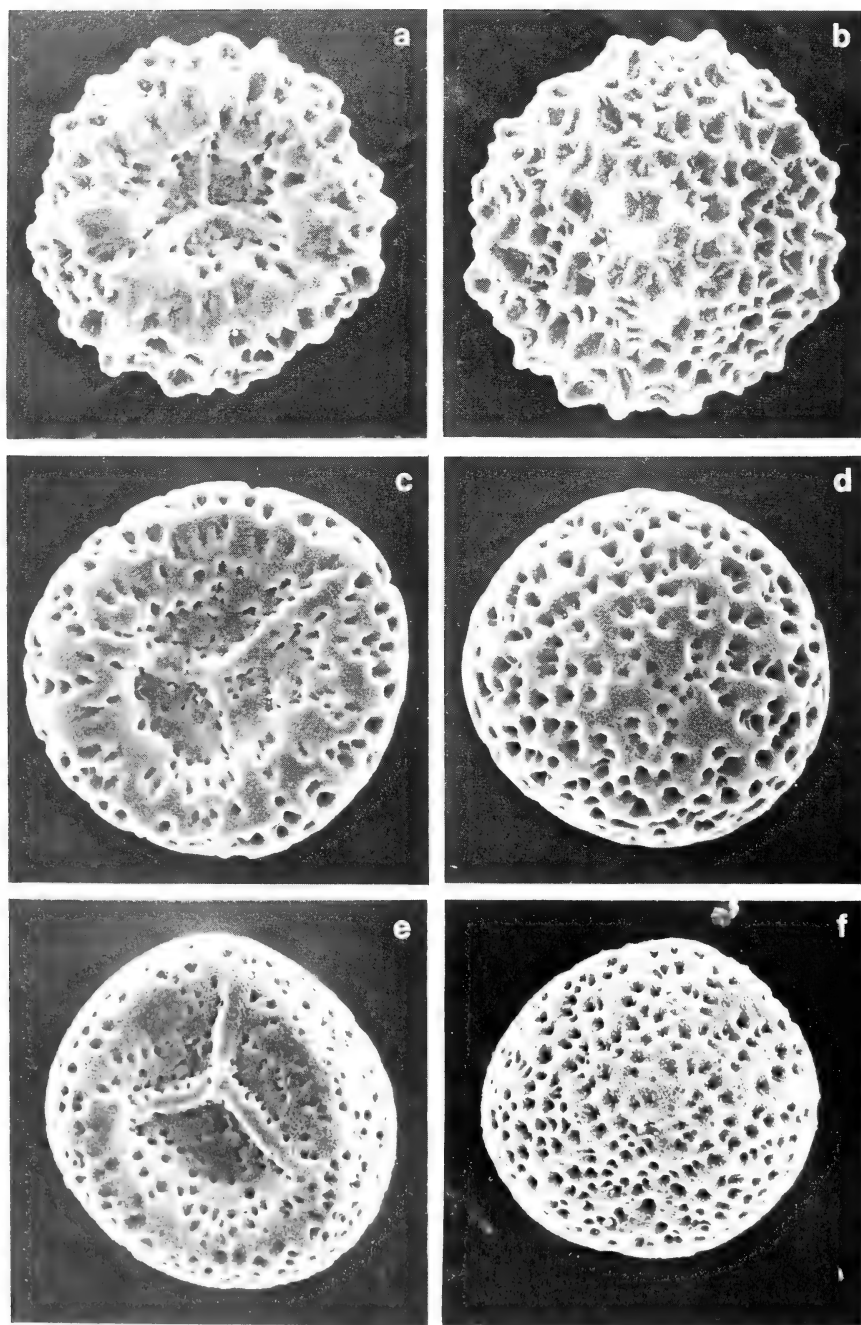


FIGURE 5. SEM photographs of *Ophioglossum* spores. All x1300. a,b, *O. vulgatum*, M. Bell, July 1977, Aston Clinton, Buckinghamshire; a, proximal view and b, distal view. c,d, *O. azoricum*, F. Townsend, June 1863, St. Agnes, Scilly Isles; c, proximal view and d, distal view. e,f, *O. lusitanicum*, M. Dawber, 21 January 1886, Guernsey, Channel Islands; e, proximal view and f, distal view. All spores untreated.

Thus, three distinct types of spore have been found in British *Ophioglossum* corresponding to the three taxa and these are shown in Fig. 5. However, there is considerable variation and thus overlap, particularly between *O. azoricum* and *O. vulgatum*, which means spore ornamentation is not a reliable character in distinguishing these two species. The spore wall surface between the pits is granular in most samples of the three species, though in some specimens the granules appear to coalesce. It is difficult to be sure that spores of equal maturity are examined in every case, and it is likely that some of the differences in the spore wall ornamentation may be attributed to different degrees of maturity, as some wall layers are not deposited until just prior to sporangial dehiscence, and layers which have been laid down may be entirely or partly lost before spores are examined (Lugardon 1978).

DISTRIBUTION AND ECOLOGY

Distribution of *Ophioglossum* in Europe

Durieu de Maisonneuve (1857) discusses at some length what was probably the first discovery in Europe of the taxon now called *O. azoricum*. It was found in two quite different French localities, Pocancy near Paris by Puel and Vigineix in 1846, and in the coastal dunes at Cap-Ferret near Arcachon in 1857 by Durieu de Maisonneuve. These discoveries caused great excitement among local botanists, who debated whether the plants were *O. lusitanicum*, a reduced form of *O. vulgatum* or indeed, a third species. The taxon was described and named a few years later by Cosson and Germain (1861) as *O. vulgatum* var. *ambiguum*.

O. azoricum has since been reported from a number of European countries, and the distribution given for this species in *Atlas Florae Europaeae* (Jalas & Suominen 1972) is western Europe, from Iceland in the north, Great Britain, Ireland and France, to the Azores, Portugal, Corsica and Sardinia in the south, and Czechoslovakia and Poland in central Europe. Other records give *O. azoricum* in Spain (e.g. Casaseca *et al.* 1982, López González 1983, Monge & Velayos 1984) and (as *O. vulgatum* f. *ambiguum*) in Italy (Fiori 1943). Lobin (1986), in his discussion of *Ophioglossum* in Macaronesia, reports *O. azoricum* from Madeira as well as the Azores, but regards reports for the Canary Islands and Cape Verde Islands as erroneous. Many of these sites are coastal or at least have an atlantic climate; others are continental, which is interesting since specimens found inland in Britain with an atlantic climate would normally be considered to be small *O. vulgatum*, and not candidates for *O. azoricum*. However, since the identity of this taxon is probably as confused in Europe as it is in Britain, these records may not reflect its true distribution.

O. lusitanicum is essentially a species of the Mediterranean region and western Europe, ranging from Portugal in the west to Turkey in the east. This is again a predominantly coastal plant with some inland stations. The third species, *O. vulgatum*, on the other hand, occurs throughout most of Europe, but is rarely found in the Mediterranean region.

Distribution and ecology of *Ophioglossum* in Britain

Ophioglossum vulgatum is relatively common throughout Britain, particularly in lowland central and south-eastern England. It is less frequent in the upland areas of Scotland, Wales and south-west England. Fronds generally appear in late April or May, mature in June or July and die down in August to September.

This species grows in a wide variety of habitats. Most commonly it may be found in old damp meadow pastures, but it also occurs on the drier chalk downlands of southern England, as well as in old chalk pits and marl pits. Damp, often peaty depressions in heathland provide a suitable habitat, as do sand-dune slacks. In E. Norfolk *O. vulgatum* grows in mown *Phragmites* mire on shallow peat over lake muds,

and the species has also been collected from the edge of a wet willow wood where it was growing in shallow water on flint shingle. Colonies are often found on sandy soils growing in association with bracken, and also in woods, copses and hedgebanks, sometimes in deep shade.

By contrast, *O. lusitanicum* is a very local species, found only in a few sites on St. Agnes in the Scilly Isles, and Guernsey in the Channel Islands. Plants may be evident above ground as early as September, maturing from November to March and dying down by the end of April. Timing depends on the seasons, which may vary considerably from year to year. This tiny fern is mainly to be found in short turf on the moist peaty or sandy soil of coastal rocky downs and cliff-tops. These sites usually face south or south-west and are relatively exposed.

Jermy *et al.* (1978) record the distribution of *O. azoricum* as Channel Islands, Scilly Isles, Lundy (Devon), Studland (Dorset), Skomer Island (Pembrokeshire), Ravenglass (Cumberland), Inner Farne (Northumberland), St. Kilda (Outer Hebrides), Dunnet Head (Caithness), and a number of sites in Merioneth, Caernarvon, Anglesey, Shetland Islands, Orkney Islands and the west coast of Ireland (Donegal, Sligo, Mayo and Kerry). These records were based on data culled from herbarium specimens, floras and field records, using the criteria of sporangial number (14 or fewer pairs), sterile blade size (less than 3.5cm long) and habitat (occurring in short turf near the sea). There are a number of specimens from other sites in various British herbaria labelled *O. azoricum*. However, I am doubtful that many of the specimens from these and well-known localities are anything other than small forms of *O. vulgatum*, and have seen more convincing specimens from inland sites in Hampshire. *O. azoricum* follows the same seasonal growth pattern as *O. vulgatum*, being evident from April to September and maturing in June or July. It is reported to grow in short, grazed turf on top of cliffs and sea crags (e.g. in Orkney), and also in sand dune slacks (e.g. at Ravenglass). These are generally damp, often exposed sites, similar to those preferred by *O. lusitanicum*.

I have seen the following specimens which are distinct in habit from *O. vulgatum* and have small fronds and relatively few sporangia thereby falling within the present concept of *O. azoricum*:

V.-c. O, Channel Islands (Guernsey, L'Ancrese Common: M. Dawber, 14 June 1884 (BM, LIV), June 1886 (DBN, NMW), 18 June 1886 (BM), 14 June 1887 (CGE), 28 May 1888 (OXF), 27 May 1890 (BM), 29 May 1890 (DBN); J.D. Gray, June 1894 (BM, CGE); W.W. Reeves, June 1885 (OXF)). V.-c. 1, Scilly Isles (W. Curnow, *sine die* (E). St. Agnes: J. Parslow, 15 May 1980 (BM); F. Townsend, June 1863 (BM). St. Martins: J. Cunnack, June 1877 (CGE), June 1881 (BM); W. Curnow, June 1877 (BM), 4 June 1877 (BM), July 1878 (BM, CGE, E, OXF); J. Ralps, June 1877 (OXF, RNG), 4 July 1877 (BM, CGE, E, K); B.V. Tellam, 1877 (BM), 3 July 1877 (BM); F. Townsend, June 1862 (CGE)). V.-c. 4, North Devon (Lundy: A. Cleave, June 1982 (BM)). V.-c. 11, South Hants (near Lyndhurst: J.M. Camus & A.M. Paul, 2 July 1985 (BM)). V.-c. 48, Merioneth (Morfa Harlech: D.A. Jones, 1 July 1898 (BM)). V.-c. 49, Caernarvon (Morfa Dinlle: R.H. Roberts, June 1961 (NMW)). V.-c. 52, Anglesey (Newborough Warren: R.H. Roberts, July 1956 (NMW)). V.-c. 70, Cumberland (Ravenglass: T. Dargie, Aug. 1971 (BM); A.C. Jermy & A.M. Paul, 14826, 26 Sept. 1980 (BM)). V.-c. 110, Outer Hebrides (St. Kilda: R.M. Barrington, June 1881 (BM). Scarp: W.S. Duncan, 26 Sept. 1890 (BM), summer 1892 (BM), July 1892 (BM). South Uist: A. Cleave, June 1983 (BM)). V.-c. 111, Orkney (Calf of Flotta: J.T. Boswell, Aug. 1880 (OXF); W.I. Fortescue, July 1878 (BM); H.H. Johnston, 2 Aug. 1878 (BM, E). Eday: H.H. Johnston, 12 July 1883 (BM). Fara: J.T. Boswell, Aug. 1880 (BM); H.H. Johnston, 20 Aug. 1880 (BM). Orphir: H.H. Johnston, 9 Sept. 1880 (OXF), 15 Aug. 1881 (BM). Swanbister: J. Boswell Syme, Aug. 1873 (BM), J.T. Syme, Sept. 1855 (BM)). V.-c. 112, Shetland (Northmaven, Brei Wick: W.H. Beeby, 6 June 1896 (BM, K, LIV). Papa Stour: W. Scott & R.C. Palmer, 19 July 1959 (OXF)). V.-c. H1, South Kerry (Great Blasket: R. Lloyd Praeger, June 1912 (BM, DBN). Three Sisters Head: R.W. Scully, 3083, July 1885 (DBN)).

DISCUSSION

Species delimitation in *Ophioglossum* is a worldwide problem. These simple plants have few characters relative to other ferns, and classifications have often been based on features which in other pteridophytes would be considered unnoteworthy. Of the

three species recognised in Britain, *O. lusitanicum* is clearly distinct in terms of growing season, size, frond shape, venation, epidermal cells and stomata, and spore ornamentation. The other two taxa, however, were found to overlap in all these respects to such an extent that many herbarium specimens could not be determined with any degree of certainty. The above features do not really help to separate *O. azoricum* from small specimens of *O. vulgatum*, though it is perhaps possible that more extensive studies might reveal significant differences between the taxa that were not evident in this study.

It is common for juvenile plants, especially ferns, to be fertile despite their small size and with a morphology often quite different from that of mature specimens. There is no reason why this should not apply to *Ophioglossum*, and it may be that some plants named *O. azoricum* are merely juvenile forms of *O. vulgatum*.

Wagner *et al.* (1981) point out that those familiar with *Ophioglossum* in the field are more likely to have reliable taxonomic opinions than herbarium workers. It is true that different populations undoubtedly appear very distinct in the field, but how much of this is due to ecotypic variation? Wagner *et al.* (1981) showed experimentally the range of variation in frond size and venation in a single species.

It seems quite possible that *O. vulgatum* would not grow as luxuriantly in exposed or heavily grazed coastal sites, as in a damp meadow, just as other pteridophyte and spermatophyte species growing in adverse conditions are stunted and different in habit to specimens in more favourable situations. An example of this may be the Hampshire specimens referred to above which grow in small damp depressions in areas regularly trampled by humans and grazed by rabbits. These plants greatly resemble coastal specimens by *O. azoricum* in size and habit. Are the Hampshire specimens true *O. azoricum*? Alternatively, are many, if not all the populations hitherto called *O. azoricum* in reality just an ecotype of *O. vulgatum*? It is interesting to note a comment by P. Taylor (unpubl. data) that he has produced plants similar to those of *O. azoricum* on Skomer Island by starving ordinary *O. vulgatum*. Miss E. Bullard (pers. comm. via A.C. Jermy) likewise considers that one would expect frond size and sporangial number to be reduced in the impoverished soils of Orkney where *O. azoricum* is found. I hope to cultivate under uniform conditions plants which appear distinct from different habitats, and also to take plants from a single population and grow them under a variety of conditions, to see if differences are maintained in the first instance or generated in the second.

The angle at which the sterile blade is held was noted to be a useful field character. Specimens of *O. azoricum* from Ravenglass and Lundy had distinctly reflexed fronds compared to the upright habit of *O. vulgatum*. This feature is, however, not clearly shown by herbarium specimens. There is an interesting series of collections from Swanbister, Orkney, made by J.T. Boswell Syme over a period of 20 years. The samples may be from more than one population, but there is a great range of variation in size. In general, the larger the specimen, the more numerous the sporangia. One sheet in particular (BM) has many specimens collected in 1855 with two fronds, sterile blades up to 50-60mm long, 20-25mm wide and up to 19 pairs of sporangia. Many of these do have distinctly reflexed fronds. Most of the other collections from 1855, 1873 and 1875 comprise smaller individuals with 7-16(-18) sporangial pairs and sterile blades 7-35 x 4-15mm. A high proportion of these have more than one frond per plant and sterile blades reflexed to some degree. Plants in the first-mentioned collection, although larger than *O. azoricum* is usually defined, do appear to have the characteristic habit of this taxon. Even this feature may be the result of the habitat; in the taller vegetation of '*vulgatum*' sites fronds are more likely to be erect and tall, whereas in the short turf of '*azoricum*' sites they are more likely to be

small and reflexed. Ecological data of any sort is often absent from herbarium specimen labels, so extensive field studies would be most useful, collecting data on frond size and habit, ecology including observations on associated species, height of vegetation etc. Photographs to accompany herbarium specimens would contribute valuable information.

In conclusion, it is evident that although there are some specimens which are distinct in size and habit from typical *O. vulgatum* and which may be confidently termed '*O. azoricum*', there are many individuals and populations intermediate between these two extremes. This prevents satisfactory separation of the two species on morphological grounds. They do not seem to be as distinct in measurable terms as the two North American varieties of *O. vulgatum* (now recognised as species) studied by Wagner (1971). Although in many respects it seems that *O. azoricum* should be synonymised with *O. vulgatum*, the fact that some populations are so manifestly distinct with their tiny reflexed leaves leads me to accept it as a separate species for the time being pending further research.

I did not find substantial evidence of *O. azoricum* being intermediate between the other two British taxa, but rather found it to be merely at one end of the range of variation exhibited by *O. vulgatum* under differing conditions. This factor, coupled with the distinctness in many ways of *O. lusitanicum* from *O. azoricum*, offers little morphological support to the proposal of the latter's hybrid origin.

As well as extensive field studies, a cytological survey of different populations of *Ophioglossum* (including those in the Azores) is necessary to help establish the status of *O. azoricum* in Britain and, indeed, Europe. If there are three cytologically different taxa involved, chromosome counts combined with morphology may enable the two problem taxa to be more satisfactorily defined.

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SHORT NOTE

ADIANTUM x *SPURIUM*, A NEW NAME FOR *A.* x *VILLOSOLUCIDUM*

In a series of papers entitled "Cytotaxonomic studies of the ferns of Trinidad" (Jermy and T. Walker, 1985, in *Bull. Brit. Mus. (Nat. Hist.)*, Botany ser. 13 (2): 133-276) the name *Adiantum* x *villosolucidum* Jermy and T. Walker, was used as an epithet for the hybrid between *A. lucidum* (Cav.) Swartz and *A. villosum* L. This hybrid was found on several occasions in Trinidad where the parents grew together, and is most likely to be found elsewhere throughout the sympatric range of the two species in the West Indies and South America.

It has been pointed out that according to Article H.10.3 in the *International Code of Botanical Nomenclature* (Voss *et al.*, 1983, Regnum Vegetabile 111, Utrecht) designations consisting of the names of the parents combined with only the termination of one epithet changed is considered to be a formula and not a true epithet. The name *villosolucidum* is therefore invalid and to rectify the mistake we propose here the following substitute:

Adiantum* x *spurium Jermy and T. Walker, **nom. nov.** based on *Adiantum* x *villosolucidum* Jermy and T. Walker, in *Bull. Brit. Mus. (Nat. Hist.)*, Botany ser. 13 (2): 256 (1985). Typus: Trinidad, Tacarigua Ward, Tunapuna, 2 mile along Caura Road, c. 60m alt., on shady bank, 3 April 1966, *M.G. & T.G. Walker* T10588 (holotype, BM: isotype herb. Walker). Paratypes: Same locality, date and collectors, T10589 (TRIN), T10590 (NY), T10591 (CR) and T10592 (BM).

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OBITUARY

CHING REN CHANG 1898-1986

Ching Ren Chang was born on 16 January, 1898, in Wujing County of Kiangsu Province. His first academic course was on forestry and he graduated from Kingling University, Nanking in 1925. For the next three years he lectured at the Department of Biology, Southeast University, Nanking. Between 1927 and 1932, Ching was Head of the Botany Section of the Metropolitan Museum, Nanking, moving to Peking, as Head of the Herbarium of the Fan Memorial Institute of Biology, in 1932 until 1945.

During these early years Ching Ren Chang started to specialise on ferns and visited the Herbarium of the Hong Kong Botanical Garden in 1926 to study the fern collections there. He followed this up with a major European visit 1929-32 during which time he studied under Carl Christensen in Copenhagen, and visited the British Museum and Kew and herbaria in Austria, Czechoslovakia, France, Germany and the Netherlands. In all of these he photographed as many fern types as he could find and this collection, now in the National Herbarium, Beijing, is an important reference database.

Between 1945 and 1955 his energies were directed to agricultural improvement, but on the setting up of the Academia Sinica in 1955 he was made a Member, and Director of the Phytotaxonomy Department of the Botanical Institute in Beijing. He continued working on ferns to the end, latterly as an Adviser of the Botanical Institute, publishing over 140 papers and books. A full list will be published in the Bulletin of Pteridology in Taxon. He has trained and inspired many young Chinese botanists and leaves a strong contingent of pteridologists in both Academia and University Departments.

Ching Ren Chang married Zuo Jin Fu in 1933, who passed away in 1964. He leaves a son, Ching Li-Ming, with whose family he lived during his last years.

A.C. Jermy & K.H. Shing

BRITISH PTERIDOPHYTE RECORDS

Compiled by A.J. Worland

The records are presented thus: 100km square/10km square followed by the recorder's name. Listed additions have been received up to the end of March 1987.

POST 1980

- 1.2 *Lycopodium clavatum* 17/52, 17/64 J. Clark. 34/19, 35/40, 35/41, 35/52
G. Halliday.
- 3.1 *Huperzia selago* 34/19, 34/28, 34/39, 35/60, 35/70, 35/71, 35/81 G. Halliday
- 4.1 *Diplazium alpinum* 17/52 J. Clark
- 6.2 *Isoetes echinospora* 07/94, 17/04, 17/26 A.C. Jermy & J. Clark
- 7.1 *Equisetum hyemale* 17/45 J. Clark
- 7.4 *Equisetum arvense* 17/05 A. Stirling
- 7.7 *Equisetum palustre* 17/05 A. Stirling
- 8.1 *Botrychium lunaria* 17/22, 17/31 J. Clark. 34/28, 35/23, 35/70, 35/80, 35/81
G. Halliday
- 9.1 *Ophioglossum vulgatum* 17/41 J. Clark
- 11.1 *Cryptogramma crissa* 17/42 J. Clark
- 14.1 *Hymenophyllum tunbrigense* 20/88 M.H. Rickard
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THE FERN GAZETTE

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THE
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Volume 13 Part 4

1988

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A CHROMOSOME COUNT FROM *AZOLLA FILICULOIDES* (AZOLLACEAE: PTERIDOPHYTA)*

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England

ABSTRACT

Azolla filiculoides has been investigated cytologically for the first time. Counts from microsporangia establish its chromosome number as $n = 22$.

INTRODUCTION

To date there have been very few cytological investigations of *Azolla* (the Water Fern). The minute chromosomes present technical problems which are compounded by the delicate nature of the roots and a scarcity of fertile material at the right stage. The extremely small chromosome size also causes considerable difficulty in the establishment of unequivocal counts. The cytology of *Azolla* has thus lagged behind research into other aspects of its biology. Recently much interest has focussed on this genus because of its nitrogen-fixing ability; this arises from the symbiotic relationship between *Azolla* and the endophytic cyanobacterium (or blue-green alga), *Anabaena azollae*, which is invariably present in the air chambers in the upper lobes of its leaves. The consequent economic importance of *Azolla* has long been recognized in the Far East, where, particularly in China and Vietnam, *A. pinnata* R.Br. has been used for centuries as a green manure for increasing the fertility of paddy fields (Lumpkin 1985). During the last ten years various other species of *Azolla* have been introduced into China for the purposes of breeding and other research, and the arrival in Leeds of Y. X. Lin presented an opportunity to count one of the most vigorous of these introduced *Azolla* species, a particularly strong-growing form identified as *A. filiculoides* Lam. *Azolla* shows much variation in the morphology of its vegetative parts, and the same species can look quite different when growing under different environmental conditions. This phenotypic plasticity has led to problems over identification; the boundaries between species are unclear and in general the taxonomy of the genus is confused.

MATERIAL

The material used in this study came originally from the Forstbotanischer Garten Eberswalde der Humboldt, at the University of Berlin in East Germany. This culture was sent to the botanic garden of the Botanical Institute, Chinese Academy of Sciences, Beijing, in 1978, and was established in cultivation there. In 1986 material of the same collection was successfully brought into cultivation at Leeds. Sporangia were produced in the autumn of 1986 and again in 1987. Material of botanic-garden origin may sometimes be misidentified, especially in view of the problems outlined above. It was therefore thought desirable to check the identification of our culture as *A. filiculoides*, and to this end various morphological features were studied. Characters for the identification of *A. filiculoides* are summarized by Ashton & Walmsley (1984) and by Ruiz de Clavijo *et al.* (1984). Fertile material of mature, well-grown *A. filiculoides*, one of two American species introduced and now widespread in Europe, is said to be very distinctive (the other, *A. caroliniana* Willd., is much more difficult to identify positively and its taxonomic status may be doubtful, see Derrick, Jermy & Paul 1987).

* Dedicated to Prof. T. Reichstein on the occasion of his 90th birthday (20.7.1987) in recognition of his friendship and encouragement.

**On leave from the Institute of Botany, Chinese Academy of Sciences, Beijing, People's Republic of China.

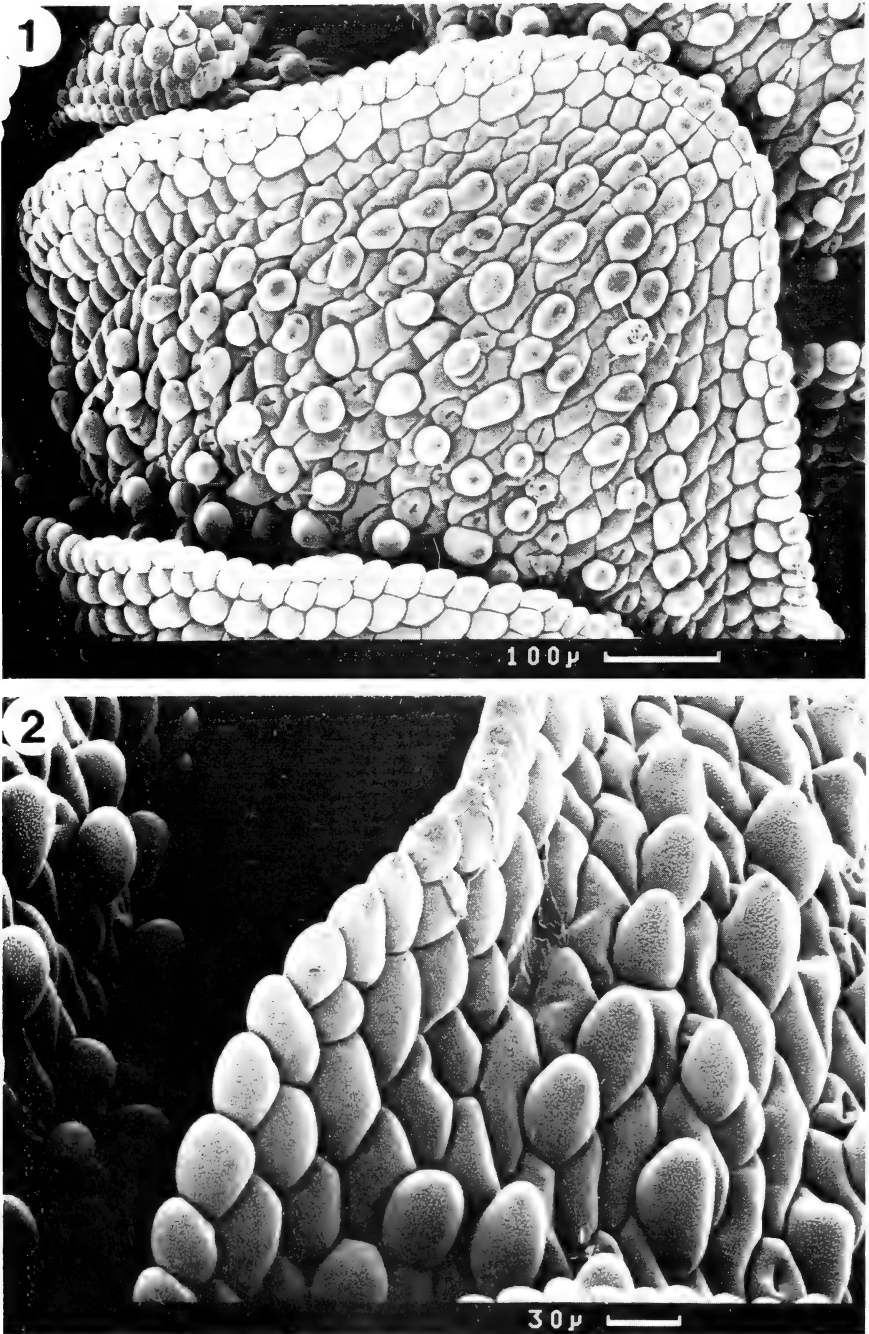


PLATE 1

I. Morphology of our cytologically attested *Azolla* material (*A. filiculoides*): SEM photographs of leaves.

Fig. 1. Upper epidermis showing the wide margin of 3-4 rows of large, hyaline cells and the central lamina bearing stomata and unicellular trichomes or papillae.

Fig. 2. Enlarged view of the unicellular trichomes.

Our material is a strong-growing plant, consisting, when mature, of both a decumbent, free-floating system as well as erect branches which can extend out of the water by as much as 5cm. When the emergent branches are well-developed the horizontal system tends to die back, forming a tangled brown mat on the water surface. The ascending growth habit arises particularly when the plant is growing in a limited space or under dry conditions. Lin (1980) has observed that on these upright branches the colourless and usually submerged lower lobes of the leaves also become green and develop *Anabaena*-containing cavities. The flattened, leafy stems of the horizontal system are elongate, and the branches distant one from another. In young plants the branching is dichotomous; on adult material unequal development at branch-points leads to a false dichotomy and branching of apparently irregular arrangement. The tips of the emergent branches tend to roll inwards to give a distinctive crisped appearance mentioned by many authors. Roots arise in no set pattern or position but acropetally at intervals along the underside of the floating stems. The ovate, imbricate, closely appressed branch-leaves agree with the description of Svenson (1944); they are alternate, greyish-green in colour, with subacute to obtuse tips and a broad, membranous margin (as described by Lawalr  e in Tutin 1964) formed of 2-3 rows of large, hyaline cells (see Figs. 1 & 2). Unicellular trichomes (Lumpkin & Plucknett 1980, Pieterse, de Lange & van Vliet 1977) are borne on the surface of the epidermis (see Figs. 1 & 2). Sporocarps develop, usually in pairs, in the axils of leaves close to the branch apices. Either two microsporocarps (very rarely, two megasporocarps) or a microsporocarp and accompanying megasporocarp occur together. Within each microsporocarp there are numerous microsporangia, each containing 4-6 massulae. The massulae bear barbed glochidia which are clearly aseptate (see Fig. 3). Fowler and Stennett-Willson (1978) attach great importance to the structure of the megaspore wall in classification; although not studied in detail the megaspore sculpturing of our material agrees well with that illustrated by them. On the basis of these observations we have no hesitation in confirming the identification of our plants as *A. filiculoides* Lam.

Voucher herbarium specimens of our material will be deposited in the national herbaria at Kew and the British Museum (Natural History), as well as in the herbaria of the Botanical Institute, Chinese Academy of Sciences, Beijing and of the International Rice Research Institute, Manila, Philippines.

METHODS

Young microsporangia were fixed in a solution of 3 parts absolute alcohol: 1 part glacial acetic acid, stained in acetocarmine and squashed according to the technique described by Manton (1950). Preparations were made permanent by McClintock's method (1929). Suitable cells were photographed in phase-contrast on a Zeiss Ultraphot II microscope. Stereoscan photographs of leaves and glochidia were taken from material fixed in 1% osmium tetroxide, dehydrated through an ascending acetone series and critical-point dried before mounting and coating with gold. The specimens were examined on a CamScan Series III scanning electron microscope.

CYTOLOGY

Several cells in metaphase I yielded counts of $n = 22$ bivalents. The cell illustrated in Fig. 4 (with accompanying explanatory diagram in Fig. 5) is at late metaphase I and some of the bivalents are already beginning to separate prior to anaphase I. One prominent pair is very much larger than the rest. Root-tip preparations by ourselves from the same material gave counts of $2n = c.44$, which are in accordance with the meiotic observations.

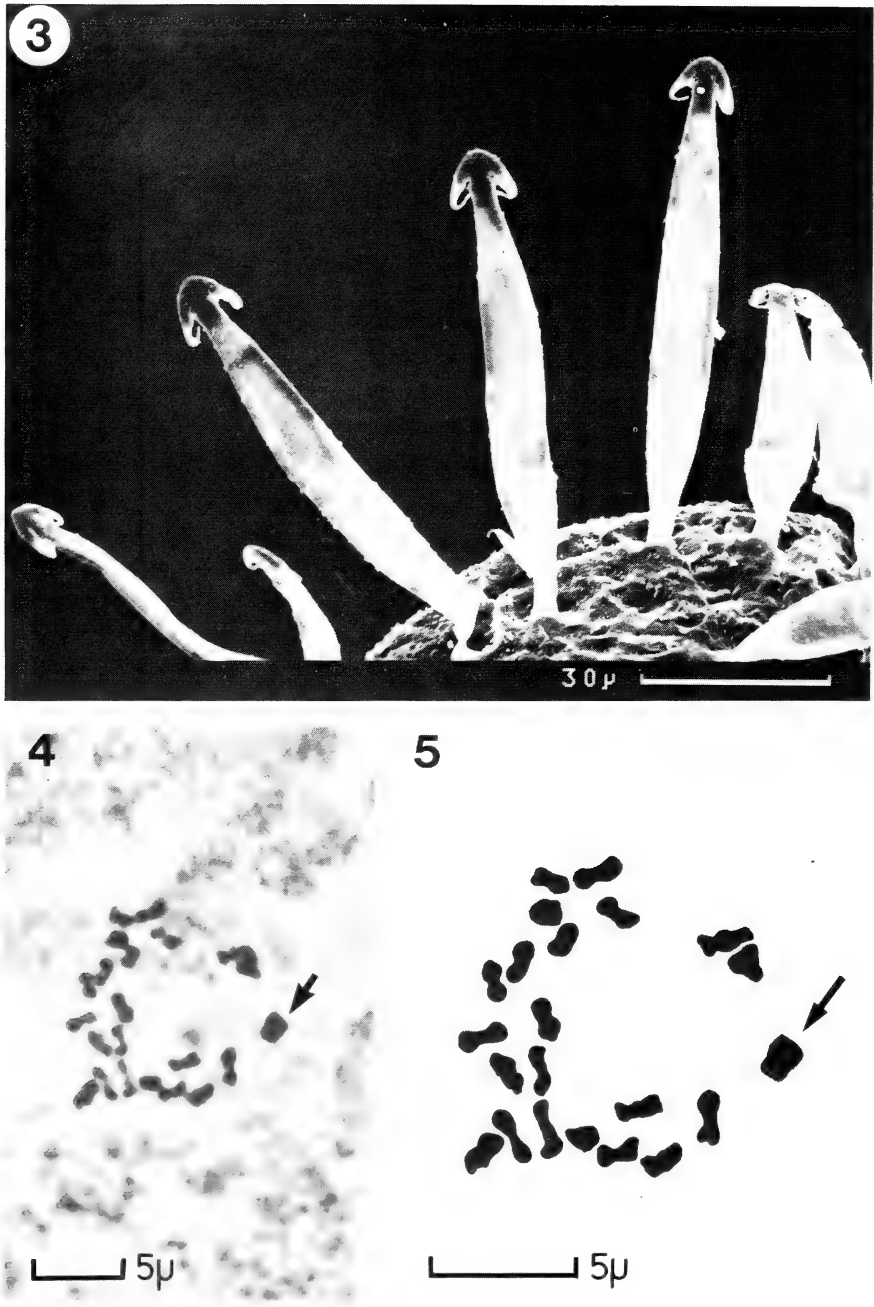


PLATE 2

Fig. 3. SEM photograph of surface of massula showing the aseptate glochidia.
II. Cytology: meiosis from microsporangium of *A. filiculoides*.
Fig. 4. Late metaphase I showing 22 bivalents. One chromosome (arrowed) is much larger than the rest. Some bivalents are already beginning to separate. Magnification: x 2,400.
Fig. 5. Explanatory diagram to fig. 4. n = 22. Magnification: x 3,800.

DISCUSSION

Löve, Löve and Pichi-Sermolli (1977) give base numbers for *Azolla* of $x = 11$, $x = 12$. The latter number is based on two early reports, the first by de Litardière (1921), who obtained a count of $2n = 48$ from material of *A. caroliniana*. He used sectioned material, from which it is not always easy to establish a precise count. However, Tschermak-Woess and Doležal-Janisch (1959), in a paper on the cytology of *Cyrtomium falcatum*, state that they found $2n = 48$ in material of *A. caroliniana*; this confirms the observation of de Litardière. Tschermak-Woess and Doležal-Janisch made counts from aceto-carmine squash preparations but they did not, unfortunately, illustrate any cells which would have confirmed their stated finding of $2n = 48$. In view of our own report of $n = 22$ from *A. filiculoides* it is highly desirable that plants referred to *A. caroliniana* should be investigated cytologically.

The practice of Löve *et al.* (1977) in deducing base numbers on purely arithmetical grounds is unsound and has already been criticized elsewhere (Walker 1977). We follow Manton & Vida (1968 p.365), quoted by Lovis (1977), in believing that the number used as a monoploid in any genus should be the lowest gametic number for which there is direct evidence. Since there is currently no evidence to the contrary, we take $x = 22$, and possibly also $x = 24$, to be the base numbers in the genus *Azolla*. The number $x = 22$ is also basic to the Osmundaceae.

Our record agrees with the counts of $n = 22$ and $2n = 44$ obtained by Loyal from both meiotic (1958) and mitotic (1975) preparations of *A. pinnata* from the Punjab. This species, like our material of *A. filiculoides*, may also be regarded as diploid. It is interesting that counts of $n = 22$ have now been recorded from each of the two sections (or subgenera) into which *Azolla* is divided: *A. pinnata* (together with *A. nilotica* Decne) is classified under section *Rhizosperma*, while *A. filiculoides* is placed in section *Azolla* (which also includes *A. caroliniana*, *A. mexicana* Presl, *A. microphylla* Kaulf. and *A. rubra* R.Br.).

The chromosomes of *Azolla* are very small in size, almost at the limit of resolution of the light microscope, and are, according to Loyal (1958, 1975), the smallest chromosomes yet recorded in the Filicales. Loyal (1975) suggests that this represents an extreme phylogenetic reduction correlated with the aquatic habit of *Azolla*. In an interesting discussion in the same paper it is also suggested that the asymmetrical nature of the karyotype (we were able to confirm Loyal's observation that the largest chromosomes are approximately double the size of the smallest ones) is linked to the high degree of morphological specialization shown by *Azolla* in its reproductive structures and its symbiotic association with *Anabaena azollae*.

Polyploidy is a common phenomenon in the homosporous ferns but, as pointed out by Klekowski & Baker (1966), it does not appear to have developed to any appreciable extent in the heterosporous Pteridophyta (Selaginellaceae, Isoetaceae, Marsileaceae and Salviniaceae), where the cytological counts available so far reveal generally low numbers and remarkable uniformity. Many more counts have been made in the homosporous ferns and, as further material is studied, the presence of polyploidy in the heterosporous Pteridophyta, recently confirmed in *Selaginella* (M. Gibby pers. comm.), may prove to be more widespread. In this connection, it is interesting to note that in the genus *Salvinia* a pentaploid hybrid has been recorded by Tatuno & Takei (1969). Only further chromosome counts will settle the question of the base number of *Azolla*, and will reveal if any polyploid strains exist. To this end various species and strains of *Azolla* have already been introduced into cultivation at Leeds for further study. In the meantime it is hoped that this preliminary report and discussion of the literature will stimulate research into different aspects of the cytology of this

tantalizingly difficult genus.

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CYTOLOGICAL AND ANATOMICAL OBSERVATIONS ON *TMESIPTERIS* (TMESIPTERIDACEAE: PTERIDOPHYTA) SPECIES FROM NEW CALEDONIA

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ABSTRACT

Cytological and anatomical observations on three of the four species of *Tmesipteris* recognised in New Caledonia are presented. The tree fern epiphytes, *T. lanceolata* Dang. and *T. sigmatifolia* Chinn., are tetraploid ($n = 104$) with sclerenchymatous pith cells in the aerial shoot and the terrestrial *T. oblanceolata* Copel. subsp. *linearifolia* subsp. nov. is octoploid ($n = c.208$) with a parenchymatous pith. No material of the fourth species, the terrestrial *T. vieillardii* Dang., was available during the present investigation but its stem anatomy showing a parenchymatous or collenchymatous pith is well documented in the literature. The chromosome numbers and pith types fall into the same patterns as those previously reported in the literature for other members of the genus from Australia, New Zealand, Solomon Islands and Vanuatu. From the evidence available at present for the genus as a whole, the chromosome number does not appear to be correlated with either pith type or ecology of the species. There is perhaps a closer, though not complete, correlation between pith type and ecology but the significance of this observation is at present not clear.

INTRODUCTION

The polyspecific nature of the genus *Tmesipteris* first put forward last century (Brown 1806, Endlicher 1833, Dangeard 1890-91) is now widely accepted (Wakefield 1944, Barber 1957, Chinnock 1975, Braithwaite 1973, 1986). While much of the evidence comes from conventional morphological studies of herbarium specimens; cytological (Barber 1957, Braithwaite 1986), anatomical (Dangeard 1890-91, Sahni 1925, Braithwaite 1973, 1986) and field studies (Barber 1957, Chinnock 1975) have made a valuable contribution, particularly in Australia, New Zealand, Solomon Islands and Vanuatu. There are some anatomical observations available in the literature for the New Caledonian species (Dangeard l.c., Sahni l.c.) but up to now no information has been available on their chromosome numbers. The present paper records some cytological and further anatomical and ecological observations on the New Caledonian species.

The majority of the earlier studies of *Tmesipteris* in New Caledonia placed the different forms under the type and original species *T. tannensis* (Spr.) Bernh. (Mettenius 1861, Diels 1906, Jeanpert 1911, 1912, Bonaparte 1921). The only exception was Dangeard (1890-91) who described one very distinctive terrestrial form as *T. vieillardii*. At the same time he described *T. elongatum* and *T. lanceolatum* from Australia and recognised two earlier species, *T. tannensis* and *T. truncatum* R.Br., from Australia and New Zealand. Despite Dangeard's very detailed morphological and anatomical studies, it was not until the early 1920's that a polyspecific concept for *Tmesipteris* in New Caledonia was accepted.

Compton (1922) recognised three species, namely *T. lanceolata* Dang., *T. tannensis* (Spr.) Bernh. and *T. vieillardii* Dang. Sahni (1925) examined Compton's material anatomically and maintained *T. vieillardii*, but on the basis of similarities in their anatomy reduced all the other forms to *T. tannensis* as var. *lanceolata*, var. *typica* (*tannensis*), which was a form of *T. lanceolata*, and var. *elongata*. The last epithet referred to the material placed under *T. tannensis* by Compton (1922) and was for a time to become the name most commonly used in European herbaria for the species now known as *T. sigmatifolia* Chinn.

Author's note added in proof:

This paper was submitted in February 1987 and type set for the 1987 issue but space constraints prevented its publication in that issue. It does not, therefore, include the results subsequently reported by Patrick Brownsey and John Lovis in their excellent paper on the New Zealand species. See Brownsey, P.J. and Lovis, J.D. 1987. Chromosome numbers for the New Zealand species of *Psilotum* and *Tmesipteris*, and the phylogenetic relationships of the Psilotales. *N. Z. Jour. Bot.* 25: 439-454.

Brownlie (1969) in the most recent fern flora of New Caledonia recognised only two species, *T. lanceolata* and *T. vieillardii*. The material originally referred to *T. tannensis* by Compton (1922) and subsequently known as *T. elongata* was incorrectly reduced to synonymy under *T. vieillardii*. Chinnock (1975, 1976) showed that *T. tannensis* s.str. and *T. elongata* s. str. are both confined to New Zealand and Australia and referred the New Caledonian material to the taxon he described from New Zealand as *T. sigmatifolia*. Brownlie's *T. vieillardii* also included a third element, which is a member of the *T. truncatum* R.Br. group. This rather distinctive taxon has never been formally recognised taxonomically but was illustrated by Bierhorst (1971). It is described here as a subspecies of *T. oblanceolata* Copel., a Pacific species already recorded by the author (Braithwaite 1986) from New Caledonia.

Four species are, therefore, considered here to occur in New Caledonia; *T. lanceolata*, *T. sigmatifolia*, *T. oblanceolata* and *T. vieillardii*. Since there is no recent systematic account covering all species present on the island, the cytological and anatomical observations will be presented in the context of a brief taxonomic treatment.

MATERIALS AND METHODS

Plants of *T. lanceolata*, *T. sigmatifolia* and *T. oblanceolata* subsp. *linearifolia* were collected during a brief visit to New Caledonia in November 1971. Material of each species was pressed and dried for herbarium specimens and also preserved in 70% alcohol for anatomical studies. Synangia were fixed in the field in 1:3 acetic alcohol and despatched by air to the U.K. for storage in deep freeze.

The material for anatomical studies was embedded in paraffin wax and the sections stained in safranin and light green. Meiotic preparations from the synangial material were made using the acetocarmine squash method. Spores for measurement were taken from dried specimens and mounted in gum chloral. Voucher specimens are deposited at the Herbarium, Royal Botanic Gardens, Kew (K).

KEY TO SPECIES AND SUBSPECIES

- 1 Sterile leaves distichously arranged, ovate to ovate-oblong with acute apices; sporophylls restricted to base or lower half of leafy shoot *T. lanceolata*
- 1' Sterile leaves spirally arranged, linear or narrowly oblong to oblanceolate with obtuse rounded or truncate apices; sporophylls usually in the middle or upper two thirds of leafy shoot 2.
- 2 Leaves sigmoid with distal ends incurved 3.
- 2' Leaves straight or falcately recurved 4.
- 3 Plants epiphytic on tree fern trunks; leaves narrowly oblong (l/b ratio <5) usually broadest below the middle, apices truncate with mucro in the middle *T. sigmatifolia*
- 3' Plants terrestrial; leaves linear or very narrowly oblong (l/b ratio >5) with parallel sides or broadest above the middle, apices sharply incurved and rounded with mucro to one side almost at right angles to leaf *T. oblanceolata* subsp. *linearifolia*
- 4 Leaves narrowly oblong to oblanceolate, more or less straight *T. oblanceolata* subsp. *oblanceolata*
- 4' Leaves linear or narrowly oblong but never oblanceolate, regularly falcately recurved *T. vieillardii*

OBSERVATIONS ON THE SPECIES

Tmesipteris lanceolata Dang., Le Botaniste II: 214 (1890-91); Compton, J. Linn. Soc. Bot. 45: 461 (1922); Brownlie, Flore de la Nouvelle-Calédonie et Dépendances 3, Ptéridophytes: 12, pl. 1, f. 1 & 2 (1969); Bierhorst, Morphology of Vascular Plants: 154, f. 12-1D & E (1971); Chinnock, N.Z. J. Bot. 13: 759 (1975).

T. tannensis (Spr.) Bernh. var. *lanceolata* (Dang.) Sahni, Trans. Roy. Soc. Lond. ser. B, 213: 145, pl. 5, f. 9 & 10 (1925).

T. tannensis (Spr.) Bernh. var. *typica* Sahni, Trans. Roy. Soc. Lond. ser. B, 213: 145, pl. 5, f. 8 (1925).

A well known species recognised by all recent authors and distinguished by rather stiff ovate to ovate-oblong leaves with acute apices, sporophylls confined to the base or lower half of the leafy shoot and by the distichous arrangement of the leaves beyond the sporophylls. It is a common epiphyte usually on the trunks of *Cyathea* and *Dicksonia* species but is also found on other trunk forming fern genera (see below) which presumably provide a similar substrate.

Stem anatomy: previously investigated by Dangeard (l.c.) and Sahni (l.c.) who both reported a stele with a sclerenchymatous pith. The results of the present investigation confirm the earlier studies. A section of the aerial shoot at the top of the transition region (Fig. 2a) shows the stele made up of three or four groups of tracheids surrounding a small and rather ill defined pith composed of thick walled lignified cells. The pith cells, though not always clearly distinguishable from the tracheids and phloem elements in transverse sections, can be readily recognised in longitudinal sections by the oblique slit like pits in their side walls.

Chromosome number: $n = 104$ (Fig. 1a,b).

Spore size: (51-) 56-58 (-63) μ m long, (18-) 21-22 (-25) μ m broad.

Specimens examined: Mt. Koghi, epiphyte on *Cyathea* trunks, 800m, 11 Nov. 1971, Braithwaite 537 (BM, K); Mt. Koghi, epiphyte on trunks of *Orthiopteris firma* (Kuhn) Brownl., 750m, 11 Nov. 1971, Braithwaite 540 (BM, K).

Tmesipteris sigmatifolia Chinnock, N.Z. J. Bot. 13: 764 (1975).

T. tannensis (Spr.) Bernh. auct. Compton, J. Linn. Soc. Bot. 45: 462 (1922).

T. tannensis (Spr.) Bernh. var. *elongata* Dang. auct. Sahni, Trans. Roy. Soc. Lond. ser. B, 213: 145, pl. 5, f. 5 & 6 (1925).

T. vieillardii Dang. auct. pro parte Brownlie, Flore de la Nouvelle-Calédonie et Dépendances 3, Ptéridophytes: 12 (1969).

An epiphytic species up to 20cm long with sigmoid narrowly oblong leaves which are incurved at the distal end. It appears to be confined exclusively to tree ferns.

Stem anatomy: Sahni (1925) studied the anatomy of the aerial shoot and found it essentially similar to that of *T. lanceolata*. A transverse section from the top of the transition region is shown in Fig. 2b. The stele here is made up of a ring of five or six tracheid bundles and their associated phloem surrounding a clearly defined pith. The pith cells are thick walled and lignified and in longitudinal sections show oblique slit like pits characteristic of fibres. The pith is generally larger and more clearly defined than in *T. lanceolata*.

Chromosome number: $n = 104$ (Fig. 1c,d).

Spore size: No mature spores were available for measurement.

Specimen examined: Montague des Sources, epiphyte on trunks of *Dicksonia baudouini* Fourn., 900m, 10 Nov. 1971, Braithwaite 529 (BM, K).

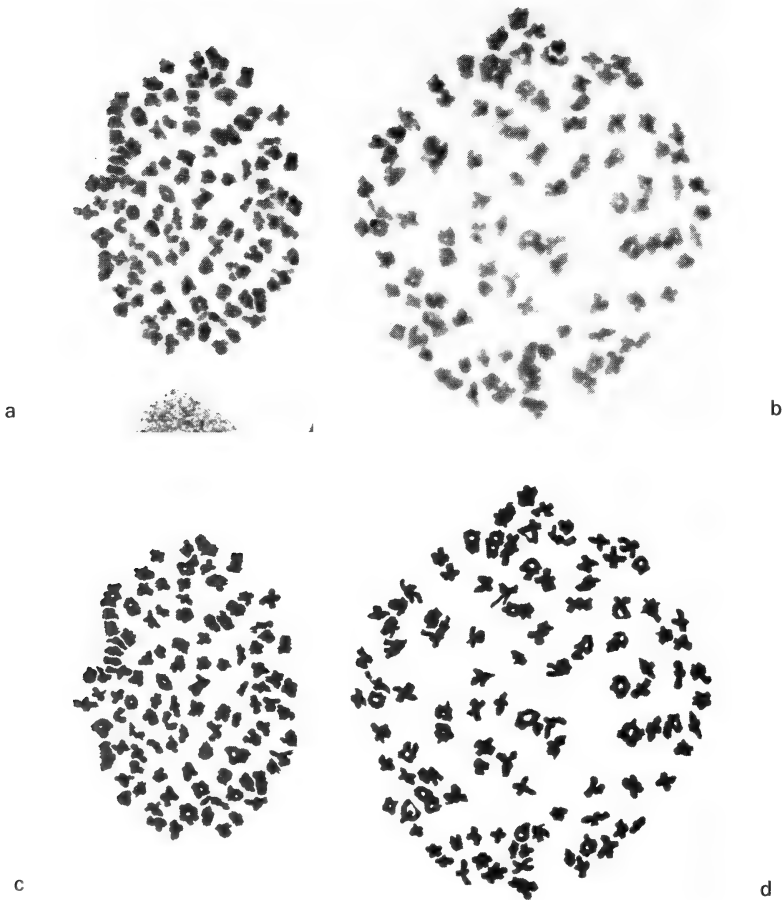


FIGURE 1. Permanent acetocarmine preparations of meiosis. X 750. a) *T. lanceolata*, Braithwaite 537. b) Explanatory diagram showing 104 bivalents. c) *T. sigmatifolia*, Braithwaite 529. d) Explanatory diagram showing 104 bivalents.

Tmesipteris oblancoolata Copel., Philip. J. Sci. 60: 99 (1936); Braith., Brit. Fern Gaz. 10: 296 (1973); Braith., Fern Gaz. 13: 94 (1986).
subsp. *oblancoolata*.

Plants terrestrial or epiphytic on angiospermous trees, 15-38cm long. Leaves 10-16mm long, 2.5-3.5mm broad, narrowly oblong or rectangular with a truncate sometimes bilobed mucronate apex to narrowly obovate with rounded mucronate apex. Chromosome number n = 208.

Distribution: Solomon Islands, New Caledonia, Vanuatu, Fiji, Samoa.

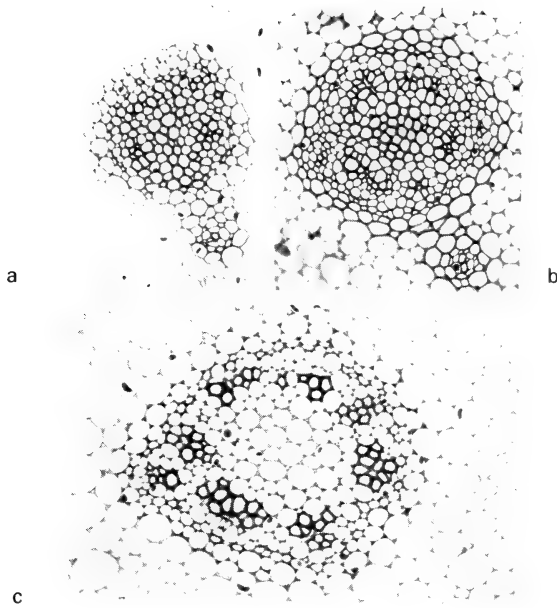


FIGURE 2. Transverse sections of aerial shoots of *Tmesipteris* species from New Caledonia. X 100. a) *T. lanceolata*, Braithwaite 540. b) *T. sigmatifolia*, Braithwaite 529. c) *T. oblanceolata* subsp. *linearifolia* subsp. nov., Braithwaite 519.



FIGURE 3. *T. oblanceolata* subsp. *linearifolia* subsp. nov., Braithwaite 519. X 1/2. Specimens preserved in alcohol.

subsp. linearifolia A. Braith. subsp. nov. Fig. 3.

T. vieillardii Dang. auct. pro parte, Brownlie, Flore de la Nouvelle-Calédonie et Dépendances, 3 Ptéridophytes: 12 (1969).

T. sp. Bierhorst, Morphology of Vascular Plants, 154, f. 12-1B & C (1971).

Plantae terrestres, erectae, 8-20cm longae. Folia 12-20mm longa, 1.5-2.5mm lata, lineares, minusve sigmoidea, interdum curvata vel tortilia irregulariter apicibus incurvatis rotundatis mucronatis; mucro setaceus, apicem surculi versum ad angulum 90. Chromosomatum numerus gametophyticae c.208.

Holotype: Plaine des Lacs, near tributary of Kuelini River, locally frequent growing out of moss on boulders and on forest floor, c. 240m, 9 Nov. 1971, Braithwaite 519 (K).

Plants terrestrial with rhizome creeping among moss on forest floor and on boulders. Aerial shoots erect, (8-) 11-18 (-20)cm long maturing in a single growing season and ending in a small leaf like appendage or if fertile in a small sporophyll; transition region (4-) 5-7 (-8)cm long; leaves and sporophylls spirally arranged, sometimes curved or twisted in different directions giving aerial shoot a rather irregular appearance and tending to decrease in length towards the apex. Leaves 12-20cm long, 1.5-2.5cm broad, linear to very narrowly oblong, slightly sigmoid, apex incurved and rounded with mucro to one side almost at right angles to the leaf and directed towards the apex of the aerial shoot. Sporophylls in upper half to two thirds of the leafy shoot, equal in length to leaves but becoming gradually reduced towards the apex. Syngangia 3-4mm long, 1.5-2.0mm high, persistent, bilocular with sporangial lobes more or less equal. Spores monoletate, concavo-convex, (70-) 78 (-87) μ m long, (26-) 31 (-36) μ m broad.

Stem anatomy: transverse sections from the top of the transition region (Fig. 2c) show the stele with a ring of 6-8 tracheid bundles surrounding a clearly defined pith composed of thin walled non-lignified essentially parenchymatous cells. This section is very similar to that illustrated by Bierhorst (1971, Fig. 12-11D) from "about halfway up the frond" of his *Tmesipteris sp.*

Chromosome number: $n = c. 208$ (Figs. 4, 5). Only a very small quantity of syngangial material was available for chromosome preparations and this yielded a few analysable, though less than perfect, cells. The interpretation of the cell illustrated shows 208 bivalents at meiosis, but there are two groups with overlapping chromosomes which are difficult to interpret with any degree of confidence. Complete accuracy for the number cannot therefore be claimed; nevertheless the error if any is not great and the order of the number is not in any doubt.

Notes: *T. oblancoolata* subsp. *linearifolia* is a generally smaller plant than subsp. *oblancoolata* with narrower linear leaves which are usually more or less sigmoid and sometimes curved or twisted in different directions giving the aerial shoots a rather irregular appearance. The rounded leaf apices with the mucro to one side and directed towards the apex of the aerial shoot are also characteristic. Field observations and ecological data on herbarium sheets indicate that it is nearly always terrestrial on the forest floor or growing on moss covered boulders.

This new subspecies belongs to the *T. truncatum* R.Br. group and may represent a consistently terrestrial form of the Australian species. It is, however, considered preferable for the time being to place it here under *T. oblancoolata* for the same reasons as those put forward by Braithwaite (1986) for referring material allied to *T. truncatum* from Vanuatu to the Pacific species.

Other specimens examined: Auf den Bergen bei Paita, 1250m, 5 Oct. 1902, Schlechter 14940 (K); Prope ortans fl. N'Go, 300m, Oct. 1912, Franc 152 (K); Source de la N'Go, 300m, Franc 468 (BM, K); Rain forest north east of St. Louis Mission, found growing from base of moss covered angiosperm tree, also in leaf base armour of low tree ferns and in other nearby places from ground litter, 540m, 20 Oct. 1947, Bucholz 1244 (K); Contrefort ouest du mó Maoya. Audessus de la Mine Emma, forêt humide, plante terrestre dressé, 1350m, 11 July 1965, McKee 12963 (K).

Tmesipteris vieillardii Dang., Le Botaniste 2: 212, t.9 & 10 (1890-91); Compton, J. Linn. Soc. Bot. 45: 462 (1922); Sahni, Trans. Roy. Soc. Lond. ser. B, 213: 143-170, pl. 5, f. 1 & 2 (1925); Brownlie, Flore de la Nouvelle-Calédonie et Dépendances, 3 Ptéridophytes: 12 (1969) pro parte; Bierhorst, Morphology of Vascular Plants, 154, f. 12-16, 12-17A (1971).

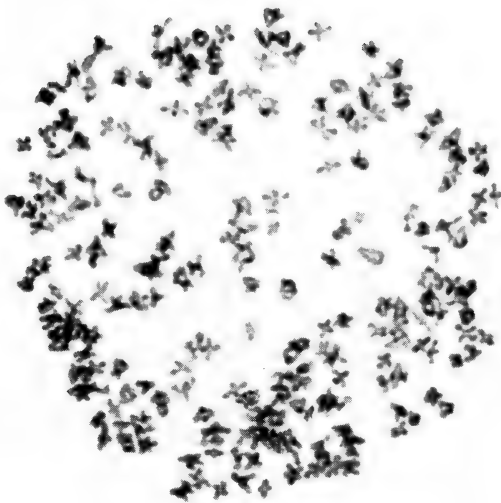


FIGURE 4. Permanent acetocarmine preparation of meiosis in *T. obanceolata* subsp. *linearifolia* subsp. nov. X 750.



FIGURE 5. Explanatory diagram for Figure 4 showing c. 208 bivalents.

This very distinctive terrestrial species, which has been recognised by all authors, is easily distinguished from all other *Tmesipteris* species in New Caledonia by its robust habit and numerous rather short stiff regularly falcately recurved leaves.

Stem anatomy: Dangeard (1890-91) and Sahni (1925) have both described and illustrated the anatomy in some detail. A typical transverse section of the aerial shoot shows a stele made up of a ring of tracheid bundles surrounding a well defined pith consisting of non lignified collenchymatous or parenchymatous cells.

Chromosome number: No material was available during the present investigation for the determination of its chromosome number. It is, however perhaps significant that both Sahni (1925) and Bierhorst (1971) reported abnormal spore production in the form of mis-shapen or abortive spores, a phenomenon confirmed by the author's own observations on herbarium specimens. The abnormal spore production could be a metabolic effect caused by temporarily adverse environmental conditions and may not be particularly significant. On the other hand it does raise the possibility of some permanent meiotic disturbance which could be the consequence of hybridisation. Cytological observations would therefore be of particular interest and may ultimately be necessary for a proper understanding of this species.

DISCUSSION

The chromosome numbers recorded here for three New Caledonian species fall into the same cytological pattern as those previously reported by Barber (1957) from Australia (and New Zealand) and Braithwaite (1986) from Vanuatu i.e. of a polyploid series based on $x = 52$ (Lovis 1977). Thus *T. lanceolata* and *T. sigmatifolia* with $n = 104$ are tetraploids and *T. oblanceolata* subsp. *linearifolia* with $n = c. 208$ is an octoploid.

A total of eleven species of *Tmesipteris* have now been investigated cytologically (Table 1) and of these, 7 are tetraploids and 4 are octoploids, but as yet no diploids have been found. Although a consistent cytological pattern for the genus appears to be emerging, it should be noted that the sampling of some species is inevitably limited by their scarcity and that others have not been sampled at all. More data are desirable particularly from New Zealand, New Guinea and the more remote Pacific islands.

The stelar anatomy of the aerial shoots of the species from New Caledonia is basically similar in so far as the stele is made up of a variable number of groups of tracheids surrounding a usually clearly defined pith. There are, however, marked differences in the nature of the pith cells. The pith of the two tetraploid species, *T. lanceolata* and *T. sigmatifolia*, is made up of thick walled lignified cells resembling sclerenchyma while that of the octoploid *T. oblanceolata* subsp. *linearifolia* is composed of non-lignified thinner walled parenchymatous cells. The last non-lignified type has also been reported in *T. vieillardii* which has not been studied in detail during the present investigation.

Variation in the type of pith cells in aerial shoots of *Tmesipteris* has been reported by a number of previous investigators. Dangeard (1890-91) divided the genus into two sections "selons qu'ils ont des fibres medullaires ou sont depourvus ...", i.e. into those species possessing a sclerenchymatous pith (*T. lanceolatum*, *T. truncatum*) and those species with a parenchymatous or collenchymatous pith (*T. vieillardii*, *T. tannensis*) or no pith at all (*T. elongatum*). In the latter case the tracheid bundles were reported to be more or less united in the centre of the stele. Sahni (1925) and Braithwaite (1973, 1986) recognised two basic types of pith composed of either lignified sclerenchymatous cells or non-lignified parenchymatous/collenchymatous cells. The different pith types reported in the literature are summarised in Table 1 together with the ecology of the species.

The ecological observations presented here on the cytologically authenticated material from New Caledonia generally confirm earlier observations in the literature

TABLE 1
Chromosome numbers, types of pith cells in aerial shoots and ecology of *Tmesipteris* species

Species	Origin	Ploidy (x=52)	Pith type	Ecology
<i>T. billiardieri</i> Endl.	Australia & Tasmania	8x1	Parenchymatous ^{2*}	Tree fern epiphyte ¹ - occ. terrestrial ⁹
<i>T. elongata</i> Dang.	Australia & Tasmania	4x1**	? No pith ²	Tree fern epiphyte ³
<i>T. lanceolata</i> Dang.	New Caledonia	4x	Sclerenchymatous ⁴	Tree fern epiphyte
<i>T. oblanceolata</i> Copel.	Solomon Islands	-	Parenchymatous ⁴	Terrestrial ⁴
	Vanuatu	8x5	Parenchymatous ⁵	Angiosperm epiphyte ⁵
<i>T. oblongifolia</i> A. Braith.	New Caledonia	8x	Parenchymatous ⁵	Terrestrial
<i>T. ovata</i> Wak.	Vanuatu	4x5	Sclerenchymatous ⁵	Tree fern epiphyte ⁵
<i>T. parva</i> Wak.	Australia	8x1	-	Tree fern epiphyte ⁶
<i>T. sigmatifolia</i> Chinn.	Australia	4x1	-	Tree fern epiphyte ⁶
<i>T. solomonensis</i> A. Braith.	New Caledonia	4x	Sclerenchymatous ⁴	Tree fern epiphyte ⁴
<i>T. tannensis</i> (Spr.) Bernh.	Solomon Islands	-	Sclerenchymatous ⁴	Tree fern epiphyte ⁴
<i>T. truncata</i> R.Br.	New Zealand	4x1***	Parenchymatous ⁷	Angiosperm epiphyte or terrestrial ³
<i>T. vanuatenensis</i> A. Braith.	Australia	8x1	Sclerenchymatous ²	Tree fern epiphyte - occ. terrestrial ¹⁵
<i>T. vieillardii</i> Dang.	Vanuatu	4x5	Sclerenchymatous ⁵	Tree fern epiphyte ⁵
	New Caledonia	-	Parenchymatous or collenchymatous ^{2,8}	Terrestrial ⁸
* Recorded as <i>T. tannensis</i> (Spr.) Bernh.				
** Recorded as <i>T. tugana</i> Barber				
*** Recorded as <i>T. fowerakeri</i> Barber				
Sources of data :	1 Barber (1957)	2 Dangeard (1890:91)	3 Chinnock (1975)	4 Braithwaite (1973)
	5 Braithwaite (1986)	6 Wakefield (1944)	7 Sykes (1908)	8 Sahni (1925)
	9 Jarman et al.(1986)			

on these species. Thus *T. lanceolata* and *T. sigmatifolia* are confined exclusively to tree fern trunks whereas *T. oblanceolata* subsp. *linearifolia*, like *T. vieillardii*, is essentially terrestrial. Elsewhere the majority of *Tmesipteris* species are recorded as tree fern epiphytes but there are a few taxa which are terrestrial, like *T. oblanceolata* subsp. *linearifolia* and *T. vieillardii*, or epiphytic on angiosperms (Table 1). The most notable of

these are *T. tannensis* s. str. from New Zealand (Chinnock 1975) and *T. oblanceolata* subsp. *oblanceolata* from the Solomon Islands (Braithwaite 1973) and Vanuatu (Braithwaite 1986). These species may occasionally be found on tree fern trunks but they appear to occur predominantly on non-tree fern substrates.

The data summarised in Table 1 does not suggest any correlation between the chromosome number and either the anatomy or the ecology of the species. The tetraploid species have either a sclerenchymatous pith or non-lignified parenchymatous/collenchymatous pith, with the former type predominant, and are found on tree fern and non-tree fern substrates. Both anatomical and ecological types are also found among the octoploid species. There is perhaps a closer, though not complete, correlation between pith type and ecology of the species. All those species listed in Table 1 growing on tree fern trunks, apart from *T. billardieri*, have a sclerenchymatous pith and those on non-tree fern substrates, whether as an angiosperm epiphyte or terrestrial fern, have a non-lignified parenchymatous/collenchymatous pith. The significance of this observation is at present not clear. It may merely be an effect of inadequate sampling. On the other hand it could be related somehow to the size of the plants or to the different functional requirements of aerial shoots in the terrestrial or angiosperm epiphytic environments as opposed to the rather specialised environment of tree fern trunks. It is not possible to reach a firm conclusion from the present incomplete data. Further studies of species not included in Table 1 are needed as well as confirmation of some of the older observations on some of the species listed there.

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SHOOT TEMPERATURE MEASUREMENTS OF MONTANE *CYATHEA* (CYATHEACEAE: PTERIDOPHYTA) SPECIES IN PAPUA NEW GUINEA

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ABSTRACT

Scales occur on the crozier and dorsal surface of the shoot apex in *Cyathea* spp. and dead frond bases are found on the lateral surfaces of the apex. Diurnal temperature measurements were made on plants growing at approx. 3500m.a.s.l. in order to determine whether these external structures are effective in protecting active tissues from low nocturnal temperatures in the tropicalpine environment.

At dawn air temperatures of 0-2°C, the croziers and pinnae of *C. gleichenioides* and *C. atrox* var. *atrox* were generally less than ambient with sub-zero temperatures recorded on occasion. Internal shoot apex temperatures, however, were consistently found to be 2.0-3.5°C above air temperature suggesting that the apical meristem is protected by surrounding structures from the potentially deleterious effect of low nocturnal temperatures.

Subsequent daytime temperature recordings revealed that the shoot apex and, to a lesser extent, the crozier tissue were slow to equilibrate to increasing air temperature. Croziers were substantially shaded by mature fronds but on receipt of direct irradiation, at around midday, showed an increase in temperature of approx. 5°C above ambient. Such a temperature increase will enhance the rate of crozier growth and development within this low temperature environment.

INTRODUCTION

The alpine regions of tropical high mountains are exposed to a high amplitude of diurnal temperature change but with little variation from season to season. The "giant rosette" plants represent an adaptation to this environment with representative examples in the genera *Espeletia* in the Andes and *Dendrosenecio*, *Lobelia* and *Senecio* occurring in the East African mountains. In these species the apical bud is surrounded by young developing leaves which show nyctinastic leaf movement, apparently serving to protect the shoot apex from low nocturnal temperatures which are frequently sub-zero (Smith 1974; Larcher 1975; Hedberg & Hedberg 1979; Beck *et al.* 1982; Rada *et al.* 1985). In addition, the layer of dead leaves which remain attached to the stem in *Espeletia* provides thermal insulation thus preventing freezing temperatures from reaching active tissues (Smith 1979; Goldstein & Meinzer 1983; Rada *et al.* 1985). The occurrence of this life-form on two widely separated mountain ranges is frequently considered to be an example of convergent evolution.

"Giant rosette" plants, however, are not found in the Papuasian mountains but *Cyathea* spp. occur commonly in exposed sub-alpine grassland to an altitude of approx. 3800m.a.s.l. where sub-zero nocturnal temperatures can occur (Wade & McVean 1969; Hnatiuk *et al.* 1976; Hope 1980). The lateral surfaces of the shoot apex are composed of dead frond bases and dense scales clothe both the flat dorsal surface of the apex and the young developing fronds. The measurements reported in this paper were planned to determine the effectiveness of these external structures in insulating active tissues from low nocturnal temperatures.

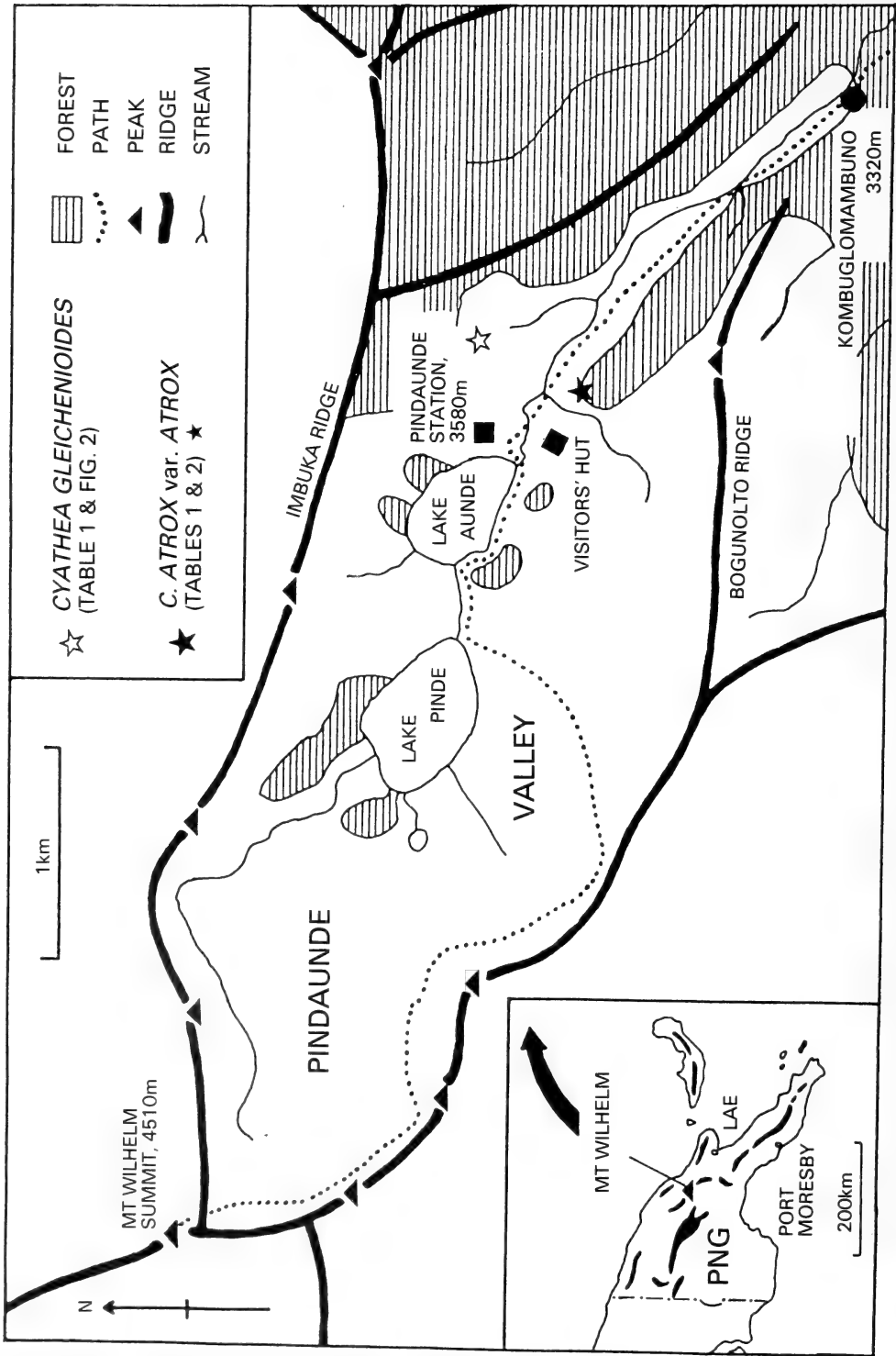


FIGURE 1. Pindaunde Valley, Mt Wilhelm. The inset of Papua New Guinea shows the major mountain ranges (after Hnatiuk *et al.* 1976 with altitudes from Humphreys 1984).

MATERIALS AND METHODS

The study was conducted on Mt. Wilhelm, Papua New Guinea near the Pindaunde Research Station (5°47'S, 145°03'E; 3580m.a.s.l.) as depicted in Fig. 1. The Pindaunde Valley is a hanging, U-shaped valley located on the south eastern flank of Mt Wilhelm. Climatic records for Pindaunde Research Station (Hnatiuk *et al.* 1976) show mean annual minimum and maximum temperatures of 4.0°C and 11.6°C respectively at screen height (1.5m above ground) with infrequent sub-zero temperatures recorded. However, the ground surface in open areas has a more rigorous temperature regime with mean annual minimum and maximum temperatures of about 1.1°C and 19.7°C and a minimum recorded extreme of -9.1°C. Freezing air temperatures are also common at canopy level (0.5-1.0m above ground) in exposed situations.

Taxonomy of the tree fern spp. involved in the present study is that of Holttum (1963) and Holttum & Edwards (1983). The vegetation of the Pindaunde Valley (Fig. 1) consists of sub-alpine tussock grassland, often with extensive tree fern shrublands, and sub-alpine rainforest which is confined to the valley sides (Wade & McVean 1969). The lower part of the Valley at Kombuglomambuno contains the montane tree fern alliance as described by Hope (1980) and is dominated by *Cyathea atrox* C.Chr. which also occurs commonly in the forest. The sub-alpine tree fern alliance (Hope 1980) occurs at approx. 3400-3800m.a.s.l. and is dominated by *C. gleichenioides* C.Chr. and *C. muelleri* Bak. which are generally not found in the forest.

Detailed diurnal time course measurements were made of shoot temperatures in single plants of *C. gleichenioides* and *C. atrox* var. *atrox* (see Fig. 1 and Table 1) generally at 30 minute intervals. Irradiance readings were taken with a miniature tube solarimeter (Delta-T, Cambridge, UK) previously calibrated with a Kipp and Zonen "Solarimeter". Total irradiance was determined in an unobstructed position in the open and irradiance reaching the croziers and dorsal surface of the shoot apex measured by placing the solarimeter at a height of approx. 20cm above the apex. Crozier and pinna surface temperatures were recorded using copper-constantan thermocouples (Comark, Rustington, Littlehampton, West Sussex, UK) linked to Wescor HR33T microvoltmeters (Wescor Instruments, Logan, Utah, USA). Crozier tissue temperature was recorded using a fixed thermocouple inserted into the tissue in the centre of the terminal coil at least 24 hours prior to taking readings. The croziers utilised were 9cm in height in the case of *C. gleichenioides* (Fig. 2) and 2cm in height for *C. atrox* var. *atrox* (Table 2). Internal shoot apex temperatures were measured with thermistors (Edale thermistor Model K, Edale Instruments (Cambridge) Ltd., UK). Thermistors were located at least 24 hours prior to reading in the centre of the dorsal surface of the apex and/or laterally approx. 10cm below the dorsal surface. Thermistor depth was 5cm for *C. gleichenioides* (Fig. 2) and 9cm for *C. atrox* var. *atrox* (Table 2).

TABLE 1. Location and characteristics of the *Cyathea* individuals utilised in this study (see also Fig. 1).

	<i>C. GLEICHENIOIDES</i>	<i>C. ATROX</i> var. <i>ATROX</i>
Altitude, m.a.s.l.	3470	3500
Location	Tussock grassland	Rainforest edge
Aspect	Fully exposed	Fully exposed
Shoot height, cm	102	410
Shoot apex diameter, cm	26	29
Mature fronds per plant	21	12
Mature frond length, cm	94	174

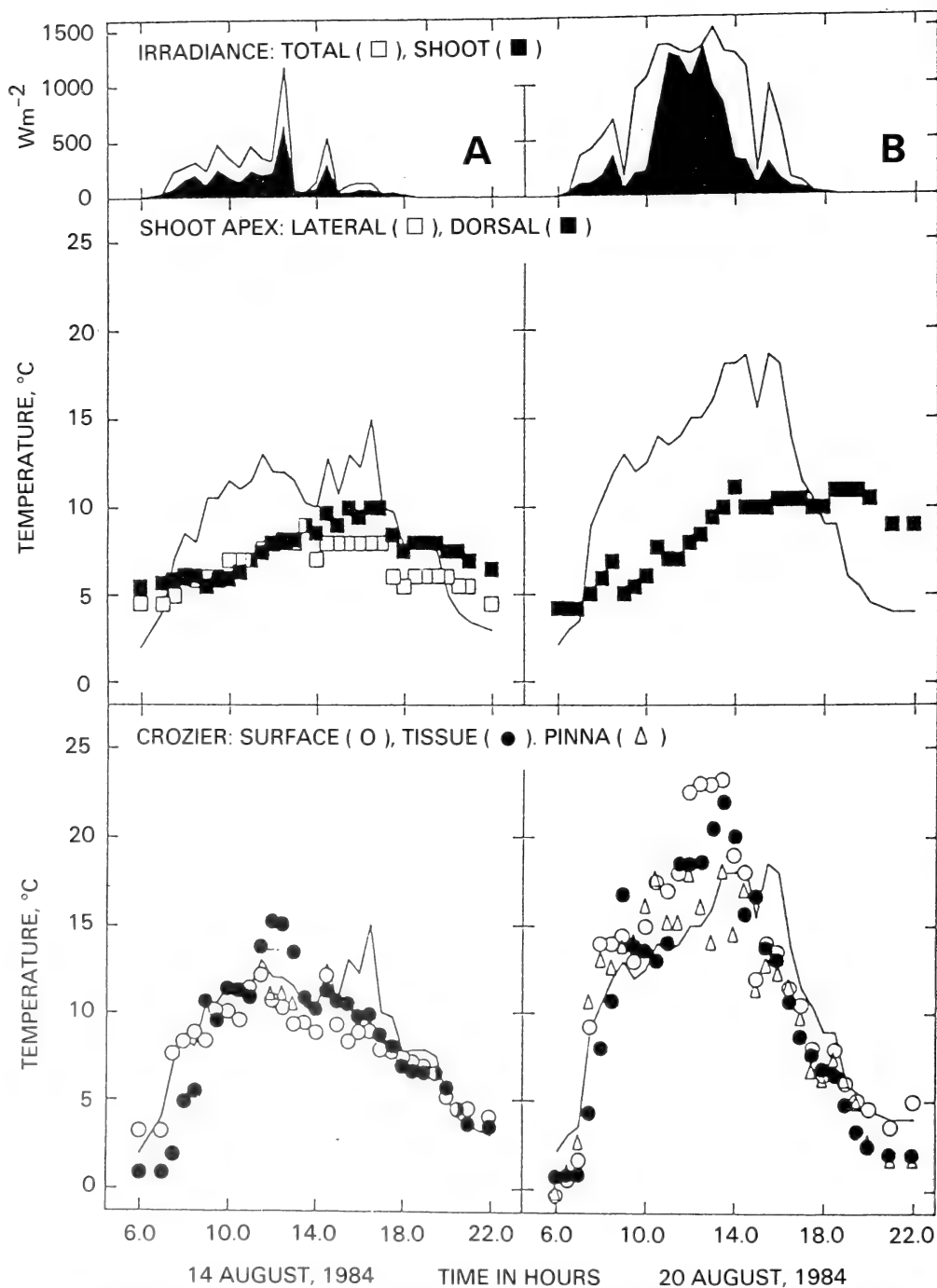


FIGURE 2. Shoot temperature recordings of the same individual of *Cyathea gleichenioides* on a cloudy cool day (A) and on a clear warm day (B). Solid lines on the graphs of shoot temperature depict air temperature. For the sake of clarity, data points for pinna temperature have been omitted on the cool day (A) except for the period of maximum irradiance. Minimum ground surface temperatures recorded at 6.00 hours were -3.0°C (A) and -1.0°C (B).

TABLE 2. Sample shoot temperature recordings of *Cyathea atrox* var. *atrox* on a clear warm day (22 August, 1984). The data are taken from a detailed time course as in Fig. 2. The minimum ground surface temperature recorded was -1.0°C at 6.30 hours.

TIME	IRRADIANCE, Wm^{-2}		TEMPERATURE RECORDINGS, $^{\circ}\text{C}$				
Hours	Total	Shoot apex	Air	Shoot apex	Pinna	Crozier surface	Crozier tissue
6.00	0	0	0.1	3.5	0.1	-0.3	-0.4
10.00	720	380	11.7	7.0	12.5	13.0	8.9
14.00	1360	945	17.0	16.5	17.0	22.0	22.2

RESULTS

Figure 2 depicts temperature recordings of various shoot tissues of a single individual of *C. gleichenioides* on a cloudy cool day and on a clear warm day.

Irradiance measurements on the cool day (Fig. 2A) showed shading by mature fronds of the dorsal surface of the shoot apex and attendant croziers. The internal temperature of the shoot apex at dawn was greater than air temperature by $2.5\text{--}3.5^{\circ}\text{C}$. Thereafter, the shoot apex slowly reached a maximum temperature in the afternoon, which was rather higher underneath the dorsal surface, but generally remained below ambient temperature. During the evening, the decline in shoot apex temperature was much less rapid than the fall in air temperature (see also Fig. 2B). Surface temperatures of the crozier were equal to or less than ambient throughout the day but the post-dawn increase in crozier tissue temperature lagged behind the increase in air temperature. Unexpectedly, the brief period of higher irradiance produced an increase in crozier tissue temperature of approx. 4°C above crozier or pinna surface temperature.

A further set of measurements was taken on a warm day (Fig. 2B) in order to investigate further the midday increase in crozier tissue temperature. Figure 2B shows that the crown and young croziers were substantially shaded by the surrounding mature fronds except for a period around midday (approx. 11–14 hours). Nocturnal and dawn temperatures of the pinna and crozier were generally less than air temperature in contrast to internal shoot apex temperatures which were well above ambient. Interestingly, the maximum shoot apex temperature was little higher on the warm day (Fig. 2B) than that occurring on the cool day (Fig. 2A). Morning temperatures of the crozier and pinna were mostly above air temperature on the warm day (Fig. 2B). The midday period of more or less unobstructed irradiance at the shoot apex increased crozier temperatures substantially above that of the air or pinna surface with the crozier surface temperature being higher than the tissue.

Similar determinations were also carried out with *C. atrox* var. *atrox* on a clear warm day (Table 2) and confirm the major findings for *C. gleichenioides* on a similar day (Fig. 2B). The internal shoot apex of *C. atrox* var. *atrox*, but not the crozier, was protected against low nocturnal temperatures and the post-dawn increase in shoot apex and crozier tissue temperature showed a lag with respect to ambient. However, the shoot apex of *C. atrox* var. *atrox* attained a higher maximum temperature (Table 2) than *C. gleichenioides* (Fig. 2B) probably due to a reduced density of scales on the dorsal surface producing a less well-insulated structure. A similar shading effect of the shoot apex of *C. atrox* var. *atrox* occurred as in *C. gleichenioides* (Fig. 2B) but the midday period of high irradiance caused an increase in crozier temperature of approx. 5°C above air or pinna temperature (Table 2).

DISCUSSION

The most unexpected finding in this work was the increase in crozier temperature of approx. 5°C above ambient in response to direct irradiation (Fig. 2 and Table 2), a feature previously observed in other bulky plant organs. Daytime temperatures of leaf and stem succulents can rise up to 20°C above air temperature giving rise to tissue temperatures as high as 60°C (Patten & Smith 1975; Nobel 1978; Larcher 1980; Kappen 1981). As the degree of succulence increases there is a decrease in the rate of heating but a greater retention of energy (Mellor *et al.* 1964). An increase in daytime temperature also occurs in the apical region of *Espeletia* which has been ascribed to the parabolic configuration of the leaf rosette thus concentrating incoming radiation to the centre (Smith 1974; Larcher 1975; Hedberg & Hedberg 1979). Recent work on *Espeletia schultzei* Wedd. has demonstrated an increase in the vertical orientation of the central rosette leaves at higher altitudes together with a more pronounced curvature of the leaf bases towards the main axis (Meinzer *et al.* 1985). It was suggested that this morphological change may enhance the capture and retention of incident radiation by the apical bud leading to more favourable temperatures for apical growth and leaf expansion.

Temperature increases in the above bulky plant organs arise as a result of a large heat capacity relative to a small surface area available for heat dissipation. In comparison to many succulents, the relatively high surface area: volume ratio of the *Cyathea* crozier produced a relatively fast heating rate but only limited energy retention (Fig. 2). In ferns, crozier uncoiling involves elongation of the rachis and differential cell elongation on the abaxial and adaxial surfaces and is mediated by polar transport of auxin produced in the pinnae (Briggs & Steeves 1958, 1959; Steeves & Briggs 1960; Voeller 1966). It seems likely that enhanced daytime temperatures of the crozier of *Cyathea* spp. will enhance the rate of crozier development in plants growing in this low temperature environment.

Nocturnal temperatures of both the crozier and pinna of *Cyathea* spp. tended to be lower than ambient and on occasion were sub-zero (Fig. 2 and Table 2). These reduced tissue temperatures were presumably due to energy exchange with the surrounding air via long-wave infra-red emission which is a common feature of the tropicalpine environment (Beck *et al.* 1982; Rada *et al.* 1985). The scales of the crozier, therefore, appear to play no part in protecting the tissue from low nocturnal temperatures. Similarly, the pubescent layer on the lower leaf surfaces surrounding the night-bud in some "giant rosette" plants does not decrease infra-red emission (Beck *et al.* 1982; Rada *et al.* 1985).

By contrast, the microenvironment of the large shoot apex of mature sporophytes of *Cyathea* spp. was relatively constant in temperature, particularly in the case of *C. gleichenioides* (Fig. 2), and protected from low nocturnal temperatures (Fig. 2 and Table 2). Stem temperatures of *Espeletia* spp. also remain above air temperature during the night with marked insulation being provided by the dead leaves (Smith 1979; Goldstein & Meinzer 1983; Rada *et al.* 1985). Experimental removal of the layer of dead leaves increases plant mortality which appears to be due to the effect of sub-zero temperatures on water availability (Smith 1979; Goldstein & Meinzer 1983). Although sub-zero nocturnal air temperatures at heights >1m above ground level were not recorded in the Pindaunde Valley in the present study (Fig. 2 and Table 2), freezing air temperature below this height are common (Hnatiuk *et al.* 1976). Young *Cyathea* sporophytes clearly have to contend with a more rigorous temperature regime than mature individuals implying that these species must possess some degree of resistance to freezing stress. Andean "giant rosette" plants avoid freezing by means

of supercooling and do not tolerate ice formation within the tissues (Larcher 1981; Rada *et al.* 1985). On the other hand, the Afroalpine species are able to tolerate freezing to the extent that full photosynthetic capacity is regained immediately after thawing (Beck *et al.* 1982, 1984; Schulze *et al.* 1985). A comparable investigation into freezing resistance of Papuanian *Cyathea* spp. clearly needs carrying out.

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PTERIDOPHYTES OF ZARATE, A FOREST ON THE WESTERN SIDE OF THE PERUVIAN ANDES

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ABSTRACT

Twenty-three species of pteridophytes are reported from an area located on the western slopes of the Andes in central Peru, which has been proposed as a nature reserve. A taxonomic key is provided. Habitats and microhabitats of the area are described. Biogeographical elements are discussed.

INTRODUCTION

The vegetation of the western slopes of the Andes in central Peru has been considered as semidesert and steppe (Weberbauer 1936, 1945; Tryon 1960, 1971). In 1952, H. and M. Koepcke discovered a small forest, called "Zárate", on a very steep lateral valley of the Rimac river. Later, the Koepckes found other smaller forests along the western slope of the Andes (Koepcke 1954, Koepcke & Koepcke 1958); all of them are in steep valleys of difficult access, between 2600 and 3500m elevation. These forests were considered to be an extension of the humid temperate zone (Koepcke 1954), which was first described by Chapman (1926) for Ecuador and Northwestern Peru. It is possible that in the past they formed a more or less continuous forest belt at that elevation interrupted only by rivers and reaching as far as 16°S (Koepcke 1961).

The pteridophyte flora of Zárate forest, as well as the surrounding area, was surveyed as part of the research needed to establish the area as a nature reserve. There are very few publications about the pteridophytes of western Peru. This study is the first done on the pteridophytes of the western slopes of the Andes in central Peru. Tryon (1960, 1971) made a brief reference to this area, describing general aspects of the environment. Floristic studies done by Sánchez (1965) and Vásquez (1967) refer to northern Peru, where climate and topography are different, while that of León (1983) is limited to the pteridophytes of the central coast below 1000m elevation.

THE STUDY AREA

The study area is located in the Department of Lima, between 11°53'17"-11°56'17"S and 76°25'41"-76°31'07"W (Fig. 1). The approximately 10km² area lies largely on the right side of the Seco river, which is part of the drainage of the Rimac river. The valley walls are very steep, with slopes ranging from 40° to vertical cliffs; there are several smaller V-shaped ravines. This study includes the Zárate forest, and the surrounding area down to 1500m elevation.

Bedrock in the area is volcanic in origin. Soils in general are immature, acidic, and coarsely textured in the lower elevations and in open sites in the forest. The percentage of sand in the soil tends to decrease with increasing altitude. In the forest, the soils are the most developed, being generally nitrogen rich, and slightly acidic or neutral (Franke & Valencia 1984).

Climatic data are not available for the study area. The general characteristics have been deduced from several meteorological stations at different altitudes and more or less similar latitudes (Franke & Valencia 1984). These reveal gradients in temperature and rainfall with altitude. Here the rainfall is seasonal; ninety percent of the annual

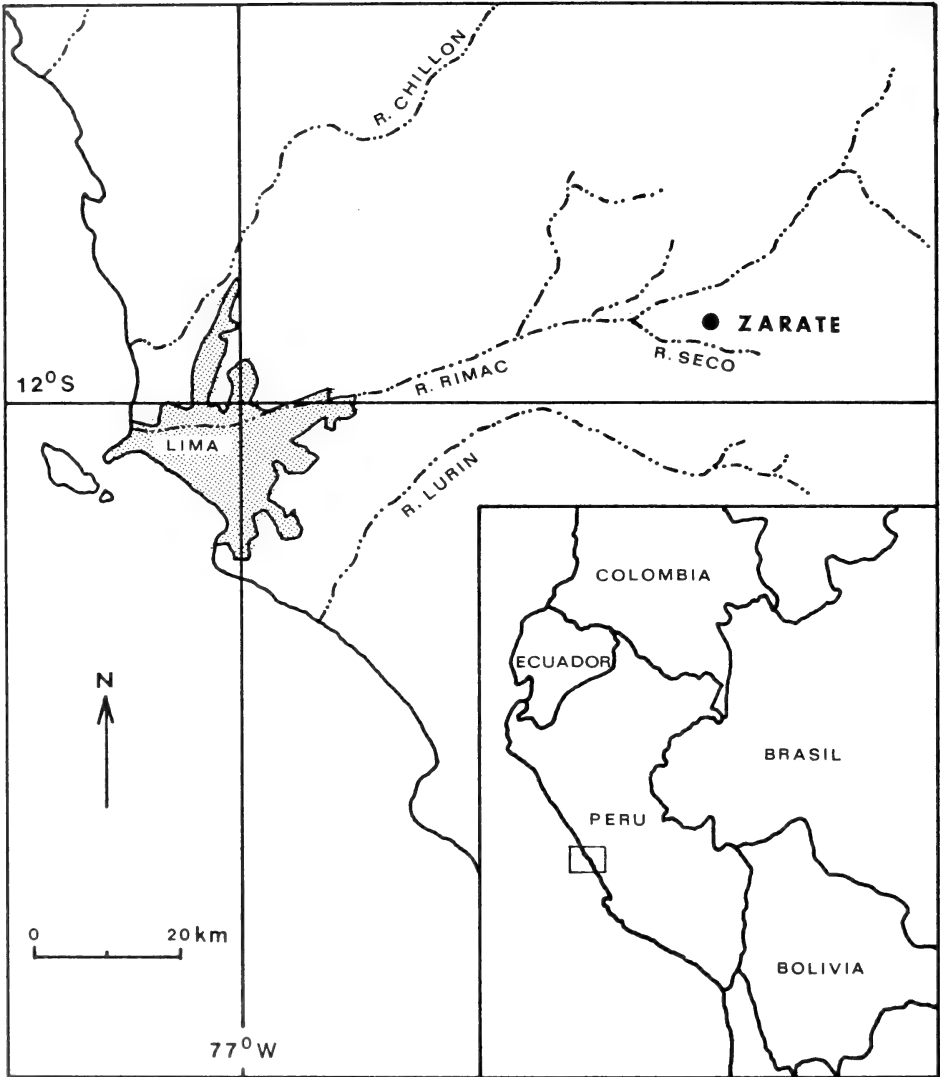


Figure 1. Map of the study area.

rainfall is concentrated during the months from November to March. In the lower parts (1500m) it is probably c. 170mm, and in the forest (2860m) it is c. 360mm. During the rainy season (southern summer) heavy mist occurs often in the forest. In the lower part of the study area, the mean monthly maximum temperature ranges from 19°C in July to 22°C in February; mean monthly minimum temperatures from 11°C in August to 14°C in March. In the forested area, the mean monthly maximum temperature ranges from 17°C in February to 18°C in July; mean monthly minimum temperature varies from 7°C in July to 9°C in March.

Most of the study area has been disturbed by human activities. For centuries the local population has probably utilized it as a source of forage and fuel. Several archeological structures are present in the forest. The lowest elevations, 1500 to 1800m, are presently used for agriculture.

METHODS

The main hiking trail crosses the altitudinal range of the study area and thus was used as a transect about 10km long. Collections were made along the trail, surveying roughly 20m to each side of it, from 1977 to 1984, by the authors, I. Franke, and A. Cano. These collections are deposited at the Herbario del Museo de Historia Natural (USM), Universidad Nacional de San Marcos, Lima. Some specimens were sent for identification to J. T. Mickel at the New York Botanical Garden (*Elaphoglossum*), and A. R. Smith at the University of California, Berkeley (*Thelypteris*). Poorly known species with nomenclatural difficulties are treated here by using the most common name found in the literature.

SPECIES LIST

Thirteen genera, twenty-three species, and three varieties have been found in the study area. A taxonomic key is provided in Appendix 1.

Adiantum digitatum Hooker

This species grows from Ecuador to Brazil and northwest Argentina. In Peru it occurs in inter-andean valleys and on the western side of the Andes between 400m and 4000m elevation. It is found in the forest of the study area in crevices among rocks.

N.V. & I.F. 23 (2700m, Cheqta, 12 Jun 1977); 1127 (2860m, Gigantón, 1 May 1981); 1273 (286m, Gatero, 1 May 1981).

Adiantum poiretii Wikstr.

This species occurs in Tropical America and in the Old World tropics. In the study area, we found two of the currently recognized varieties for Peru (Tryon 1964):

Adiantum poiretii Wikstr. var. *poiretii*

This variety occurs from Mexico, Central America and the Antilles to Bolivia and Uruguay. In Peru it grows on both sides of the Andes and in inter-andean valleys between 800m and 3900m elevation. In the study area it is commonly found in humid, shaded parts of the forest. N. V. & I. F. 514 (2850m, Mayhuayqui, 13 Jan 1980); 560; and 610 (2880m, Carnacha, 4 Mar 1980).

Adiantum poiretii Wikstr. var. *sulphureum* (Kaulf.) R. Tryon

This variety grows from Peru to Chile and Argentina, at the same altitude as var. *poiretii*. In the study area it only occurs in humid, shaded sites in the forest.

N. V. & I. F. 346 (3000m, Carnacha, 25 Mar 1978); 1277 (2860m, Gatero, 1 May 1981).

Adiantum subvolubile Kuhn

This species occurs in Ecuador and Peru. In Peru it grows in seasonal coastal vegetation ("lomas"), on both sides of the Andes and in inter-andean valleys. In the study area it has been found among rocks in sites protected by the vegetation.

N. V. & I. F. 276 (2850m, Gigantón, 25 Mar 1978); 592 (2870m, Gigantón, 4 Mar 1980); 1143 (2000m, Chunaca, 1 May 1980).

Asplenium aethiopicum (Burm.f.) Becherer (syn. *A. praemorsum* Sw.)

This species is widely distributed in the tropics of the Old and New Worlds. In Peru it occurs in the departments of Amazonas, Junín, and Cuzco, between 1200m and 3200m elevation. In the study area, it grows among rocks and in partially open sites. This is the first report of this species on the western side of the central Andes.

N. V. & I. F. 1275 (2860m, Gatero, 1 May 1981).

Asplenium fragile Presl

This species is distributed from Venezuela to Chile, above 2800 m elevation. In Peru it occurs in the departments of Cajamarca, Ancash, Junín, Lima, Huancavelica, Ayacucho, and Puno. In the study area it grows among rocks, and in humid, shaded sites in the forest.

N. V. & I. F. 763 (2870m, Gigantón, 20 Apr 1980); 1526 (3100m, Pampa Zárate, 23 Apr 1982).

Asplenium sessilifolium Desv.

This species is distributed from Mexico and Central America to Colombia, Peru and Bolivia. In Peru it has been found in inter-andean valleys between 2900m and 4000m elevation. In the study area, it occurs in humid, shaded sites, sometimes together with *A. fragile*.

N. V. & I. F. 145 (3100m, Muralla, 30 Jul 1977); 278 (2850m, Gigantón, 25 Mar 1978); 392 (2900m, Gatero, 30 Apr 1978); 541 (2850m, Gigantón, 13 Jan 1980); 638 (2888m, Carnacha, 4 Mar 1980); 891 (2870m, Carnacha, 4 Mar 1978); 1109 (2860 m, Mayhuayqui, 1 May 1981).

Cheilanthes myriophylla Desv.

This species is distributed from Mexico and Central America to Chile, Brazil, and Argentina. In Peru it occurs on the western side of the Andes, and in inter-andean valleys, between 1500m

and 3500m elevation. In the study area it has been found in rock crevices in open areas.

N. V. & I. F. 361 (2900m, Gigantón, 26 Mar 1978); 999 (2250m, Tarita, 21 Jan 1981).

Cheilanthes orbignyana Kuhn

This species has been found in Peru and Bolivia. In the study area it grows in rock crevices and protected sites, together with *Adiantum digitatum*.

N. V. & I. F. 534 (2860m, Gatero, 13 Jan 1980); 666 (2860m, Gatero, 4 Mar 1980); 1274 (2860m, Gatero, 1 May 1981).

Cheilanthes peruviana (Desv.) Moore

This species occurs only in Peru, between 400m and 3200m elevation. It grows in rock crevices of open sites, together with *Notholaena nivea* and *Pellaea ovata*.

N. V. & I. F. 352 (2860m, Gatero, 14 Jan 1980); 506 (2850m, Gigantón, 13 Jan 1980); 642 (2880m, Carnacha, 4 Mar 1980); 1276 (2870m, Gatero, 2 May 1981).

Cheilanthes pilosa Goldm.

This species occurs from Peru to Argentina. In Peru it occurs on the western side of the Andes and in inter-andean valleys, between 2800m and 4000m elevation. In the study area it grows in rock crevices and open sites.

N. V. & I. F. 1111 (2870m, Mayhuayqui, 3 May 1981).

Cheilanthes pruinata Kaulf.

This species is distributed from Peru to Argentina. In Peru it occurs on the western side of the Andes and in inter-andean valleys, between 1500m and 4200m elevation. In the study area it has been found in rock crevices.

N. V. & I. F. 345 (3000m, Carnacha, 25 Mar 1978); 533 (2860m, Gatero, 13 Jan 1980).

Cystopteris fragilis (L.) Bernh.

This is a cosmopolitan species. In Peru it has been found between 2400m and 4400m elevation. In the study area it grows in humid, shaded sites in the forest.

N. V. & I. F. 277 (2850m, Gigantón, 25 Mar 1978); 607 (2880m, Carnacha, 4 Mar 1980); 724 (3300m, Ventanilla, 28 Jul 1980).

Elaphoglossum minutum (Pohl ex Fee) Moore

This species grows in the Andes and southern Brazil. In the study area it has been found in rock crevices, protected by vegetation.

B. L. et al. 907 (2860m, Gigantón, 8 Apr 1986).

Equisetum bogotense H.B.K.

This species occurs from central America and the Greater Antilles to Chile and Argentina. In Peru it has been found between 500m and 4000m elevation. In the study area it grows commonly in humid places along running water.

N. V. & I. F. 174 (2850m, Gigantón, 28 Aug 1977); 614 (2880m, Carnacha, 4 Mar 1980).

Notholaena nivea (Poirot) Desv. var. *tenera* (Hooker) Grisebach

This species is distributed from Peru to Argentina. In Peru it occurs between 1800m and 4000m elevation. In the study area it has been found in crevices in open areas together with *Cheilanthes peruviana* and *Pellaea ovata*.

B. L. et al. 900 (2000m, Chunaca, 6 Apr 1986).

Pellaea ovata (Desv.) Weath.

This species is distributed from Mexico to Argentina. In Peru it occurs in inter-andean valleys. It has been found in rock crevices of the lower part of the study area mixed with *Cheilanthes peruviana* and *Notholaena nivea*.

B. L. et al. 901 (2000m, Chunaca, 6 Apr 1986).

Pellaea ternifolia (Cav.) Link

This species is distributed from southeastern U.S.A. to Argentina and the Hawaiian Islands. In Peru it occurs between 1600m and 4100m elevation. In the study area it grows in rock crevices in open sites.

N. V. & I. F. 531 (2860m, Gatero, 13 Jan 1980); 1110 (2880m, Mayhuayqui, 2 May 1981).

Polypodium pycnocarpum C. Chr.

This species has been found in Peru and Bolivia. In Peru it occurs from La Libertad and Ancash to Puno and Cuzco, in the seasonal coastal vegetation ("lomas") and inter-andean valleys, between 350m and 4080m elevation. In the study area it grows as an epiphyte or in rock crevices in vegetation-protected sites.

N. V. & I. F. 275 (2850m, Gigantón, 25 Mar 1978); 328 (3000m, Gigantón, 26 Mar 1978); 526 (3000m, Pampa Zárate, 13 Jan 1980).

Selaginella novae-hollandiae (Sw.) Spring

This species is distributed from Nicaragua to Bolivia. In Peru, it occurs between 350m and 3200m elevation. In the study area, it grows in humid, protected sites.

B. L. *et al.* 902 (2500m, Pascana, 6 Apr 1986).

Thelypteris glandulosolanosa (C. Chr.) R. Tryon

This species is distributed in Ecuador, Peru and Bolivia. In Peru it has been found in Junín and Lima. In the study area, it grows in exposed sites in the forest.

N. V. & I. F. 179 (2880m, Gigantón, 30 Aug 1977); 515 (2850m, Gigantón, Gigantón, 13 Jan 1980); 670 (2825m, Gigantón, 4 Mar 1980).

Thelypteris rufa (Poir.) A. R. Smith

This species occurs from Ecuador to Peru and Bolivia. In Peru it has been found in the departments of Cajamarca, Lima, and Cuzco. In the study area it grows in humid sites protected by the vegetation.

N. V. & I. F. 890 (3300m, Ventanilla, 28 Jul 1980).

Trachypteris induta (Maxon) R. Tryon & A. Tryon

This species is endemic to Peru. It has been found in the departments of Amazonas, Cajamarca, La Libertad, and Lima between 750m and 2900m elevation. In the study area, which is close to the type locality, it grows in open sites in crevices.

N. V. & I. F. 559 (2330m, Molle, 4 Mar 1980); 971 (2100m, Mital, 18 Jan 1981).

Woodsia montevidensis (Spreng.) Hieron.

This species is widely distributed in South America, from Colombia to Argentina and Uruguay. In Peru it occurs in inter-andean valleys and on both sides of the Andes above 2500m elevation. In the study area it grows in rock crevices partially protected by the vegetation.

N. V. & I. F. 277 (2850m, Gigantón, 25 Mar 1978); 344 (3000m, Carnacha, 25 Mar 1978); 568 (2830m, Gigantón, 4 Mar 1980); 638 (2880m, Carnacha, 4 Mar 1980); 1112 (2870m, Mayhuayqui, 1 May 1981); 1140 (2500m, Pascana, 1 May 1981).

DISTRIBUTION IN THE STUDY AREA

In general, the number of pteridophyte species increases with elevation in the study area, although the species composition in any site varies with local topography and microhabitats. At lower elevations (1500-2350m) only five species are present, while 20 species occur in the forest (3000m). This difference is probably due to increased humidity with altitude, and the increased number of microhabitats. The forest only covers 15% (1.5km²) of the study area, but contains 87% of the species of pteridophytes.

HABITATS

The habitats where the pteridophytes occur are referred to using the classification of vegetation previously given by Valencia & Franke (1980). The study area represents a good example of the variation in topography, altitude, and environments of the western Andes of central Peru.

Cactus Zone (1500-1950m). This xerophytic vegetation is characterized by columnar cacti (*Neoraimondia rosaiflora* (Werd. & Backbg.) Backbg., *Haageocereus acanthus* (Vpl.) Backbg.), and some seasonal forbs (*Jungia* spp., *Nicotiana* spp., *Lycopersicon peruvianum* (L.) Mill.) or cultivated fields of *Opuntia ficus-indica* Mill. Pteridophytes do not occur here.

Carica and Jatropha Zone (c. 1950-2350m). This is an association of scattered shrubs of *Carica candicans* A. Gray and *Jatropha macrantha* Muell. Arg., and a larger number of seasonal forbs (*Browallia americana* L., *Jungia* spp., *Lycopersicon peruvianum* (L.) Mill., *Nicotiana* spp., *Piqueria peruviana* (J.F. Gmel.) Robinson). In this zone we found *Adiantum subvolubile*, *Cheilanthes myriophylla*, *C. peruviana*, *Notholaena nivea*, and *Pellaea ovata*.

Croton Zone (c. 2350-2600m). This dry scrub vegetation is dominated by *Croton ruizianus* Muell. Arg. *Randia boliviana* Rusby and *Cordia macrocephala* (Desv.) H.B.K. are also important. In this zone we found the terrestrial pteridophytes *Adiantum subvolubile*, *Cheilanthes myriophylla*, *C. peruviana*, *Selaginella novae-hollandiae*, and *Trachypteris induta*. The only exception was *Polypodium pycnocarpum*, which grows on lichen/moss mats found on some of the boulders.

Thorny Scrub Zone (c. 2600-2700m). This is a transition zone from scrub vegetation to the forest. The dominant taxa are *Hesperomeles cuneata* Lindl., *Duranta pseudorepens* Mold., and *Barnadesia blakeana* Ferreyra. The pteridophytes that occur here are *Adiantum digitatum*, *A. subvolubile*, *Cheilanthes myriophylla*, *C. peruviana*, *Polypodium pycnocarpum*, *Selaginella novae-hollandiae*, and *Woodsia montevidensis*.

Oligotherme forest (c. 2700-3200m). This is floristically the richest zone in the area, consisting of three dominant tree species, *Oreopanax oroyanus* Harms., *Myrcianthes quinqueloba* McVaugh, and *Prunus rigida* Koehne, along with scattered evergreen shrubs and several seasonal herbs. Here we found *Adiantum digitatum*, *A. poiretii*, *A. subvolubile*, *Asplenium fragile*, *A. aethiopicum*, *A. sessilifolium*, *Cheilanthes myriophylla*, *C. orbignyana*, *C. peruviana*, *C. pilosa*, *C. pruinata*, *Cystopteris fragilis*, *Elaphoglossum minutum*, *Equisetum bogotense*, *Pellaea ternifolia*, *Polypodium pycnocarpum*, *Selaginella novae-hollandiae*, *Thelypteris glandulosolanosa*, *T. rufa*, and *Woodsia montevidensis*.

MICROHABITATS

Four main microhabitats could be distinguished in the study area: crevices in open areas, sites protected by the vegetation, lichen/moss mats, and humid sites. These microhabitats are dispersed mosaic fashion, in the habitats previously described. The *Carica* and *Jatropha* zone had only two microhabitats, the *Croton* and Thorny Scrub zones had three, and the Oligotherme zone had all four microhabitats.

The most important pteridophyte microhabitat was found in areas protected by the vegetation. We observed that the leaves and branches of shrubs and trees offer shade and protection at their base, keeping soil and air humidity high, and maintaining moderate temperatures. The pteridophytes which occurred here were *Adiantum digitatum*, *A. poiretii*, *A. subvolubile*, *Asplenium fragile*, *Asplenium sessilifolium*, *Cheilanthes orbignyana*, *Cystopteris fragilis*, and *Elaphoglossum minutum*. In the lower and drier zones of the study area, this microhabitat also permits pteridophytes, such as *Selaginella novae-hollandiae*, to grow together with drought-evading forbs and graminoids.

Crevices in open areas also represent an important microhabitat; they occur in rocky places or cliffs. This microhabitat probably provides soil and nutrients, and a partial protection from insolation. This type of microhabitat is especially frequent in the lower parts of the study area. Most of the cheilanthoid species, which were described by Mickel (1986) as generally occurring in dry, rocky areas, were well represented here: *Cheilanthes myriophylla*, *C. peruviana*, *C. pilosa*, *C. pruinata*, *Notholaena nivea*, *Pellaea ovata*, *P. ternifolia*, and *Trachypteris induta*. In addition, *Asplenium aethiopicum* and *Woodsia montevidensis* also occurred here.

The lichen/moss mat microsite was found on tree branches or boulders in the forest and nearby zones. The only pteridophyte in this microhabitat was *Polypodium pycnocarpum*, many individuals of which grew here as epiphytes.

The fourth microhabitat consisted of humid sites. These mainly occur in very humid rocky places and beside running water, in the upper part of the forest. *Equisetum bogotense*, *Thelypteris glandulosolanosa*, and *T. rufa* were found here surrounded by forbs.

BIOGEOGRAPHICAL ELEMENTS

We distinguish four groups of species in the study area, on the basis of types of distribution ranges: tropical-subtropical, tropical American, Andean, and cosmopolitan.

The tropical-subtropical group includes those species occurring in the tropics and subtropics of America, and elsewhere. This group contains 12 species: *Adiantum*

poiretii, *Asplenium aethiopicum*, *A. fragile*, *A. sessilifolium*, *Cheilanthes myriophylla*, *C. pilosa*, *C. pruinata*, *Equisetum bogotense*, *Notholaena nivea*, *Pellaea ovata*, *P. ternifolia*, and *Woodsia montevidensis*. The tropical American group includes those species restricted to the tropics of America. It contains only one species: *Selaginella novae-hollandiae*. The Andean group is restricted to species that occur along the Andes and contains nine species, including two endemic to Peru: *Adiantum digitatum*, *A. subvolubile*, *Cheilanthes orbignyana*, *C. peruviana*, *Elaphoglossum minutum*, *Polypodium pycnocarpum*, *Thelypteris glandulosolanosa*, *T. rufa*, and *Trachypteris induta*. The cosmopolitan group contains only *Cystopteris fragilis*.

The forest of the study area contained all the biogeographical groups, in addition to the largest number of species and of microhabitats. By including it and the surrounding area within a nature reserve, a valuable portion of the pteridophyte species of the western central Andes would be preserved, thus leaving open the possibility in the future of achieving a better understanding of the history and development of the flora of the western Andes.

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APPENDIX 1 **KEY TO THE TAXA**

A	Axes or stems without conspicuous leaves, these reduced to scales in a whorled arrangement	<i>Equisetum bogotense</i>	
A'	Axes or stems with conspicuous leaves		B
B	Axes prostrate; leaves in four longitudinal rows	<i>Selaginella novae-hollandiae</i>	
B'	Axes erect, plants not as above		C
C	Lamina entire or pinnatisect		D
C'	Lamina pinnate or pinnate-pinnatifid		F
D	Lamina entire, lanceolate	<i>Elaphoglossum minutum</i>	
D'	Lamina pinnatisect		E
E	Petiole articulate; lamina lanceolate; lamina scales brown or gold-brown, somewhat dense on the abaxial surface	<i>Polypodium pycnocarpum</i>	
E'	Petiole not articulate; lamina pedate or 3-lobed; lamina scales pinkish brown, sparse on the abaxial surface	<i>Trachipteris induta</i>	
F	Lamina with last segments of the central pinna less than 5mm long; last segments elliptic, orbicular or deltoid		G
F'	Lamina with last pinnae or segments of the central pinnae more than 5mm; last segments cuneate, flabellate or elliptic		L
G	Lamina with scales of trichomes; when glabrous then herbaceous (<i>Cheilanthes orbignyana</i>)		H
G'	Lamina glabrous, chartaceous	<i>Notholaena nivea</i> var. <i>tenera</i>	
H	Leaves scaly		I
H'	Leaves glabrescent or pubescent		J
I	Lamina usually 3-4 pinnate; segments suborbicular, less than 1mm long	<i>Cheilanthes myriophylla</i>	
I'	Lamina 1-2 pinnate-pinnatifid; segments triangular, more than 1mm long	<i>Cheilanthes peruviana</i>	
J	Lamina herbaceous, glabrescent	<i>Cheilanthes orbignyana</i>	
J'	Lamina chartaceous or coriaceous, pubescent		K
K	Axes with non-glandular trichomes	<i>Cheilanthes pilosa</i>	
K'	Axes with glandular trichomes	<i>Cheilanthes pruinata</i>	
L	Lamina with 3-4 pairs of gradually reduced basal pinnae, lamina more than 5cm wide		M
L'	Lamina generally without reduced basal pinnae, lamina less than 5cm wide		N
M	Lamina herbaceous-chartaceous; central pinnae less than 10cm long; leaves 60cm long; indusia inconspicuous	<i>Thelypteris rufa</i>	
M'	Lamina coriaceous; central pinnae 10-15cm long; leaves 100cm long; indusia conspicuous, villous	<i>Thelypteris glandulosolanosa</i>	
N	Lamina pinnate-pinnatifid, if bipinnate then chartaceous		O
N'	Lamina 2-4 pinnate, herbaceous		T
O	Segment margins entire		P
O'	Segment margins crenate or partially dentate		Q
P	Axes stramineous; pinnae petiolulate	<i>Pellaea ovata</i>	
P'	Axes dark castaneous or atropurpureous; pinnae not petiolulate	<i>Pellaea ternifolia</i>	
Q	Indusium attached by one side to the segment; pinnae bases cuneate		R
Q'	Indusium cup-like; pinnae base not as above	<i>Woodsia montevidensis</i>	
R	Lamina chartaceous, scaly; lamina scales subulate and conspicuous	<i>Asplenium aethiopicum</i>	
R'	Lamina herbaceous, glabrescent		S
S	Pinnae less than 1cm long, pinnae entire or with an acroscopic lobe	<i>Asplenium fragile</i>	
S'	Pinnae more than 1cm long, generally lobed in the acroscopic and basiscopic side	<i>Asplenium sessilifolium</i>	
T	All ultimate segments free, cuneate or flabellate; marginal false indusium		U
T'	Only some ultimate segments free, cuneate; indusium scale-like	<i>Cystopteris fragilis</i>	
U	Segments articulate; leaves sub-scandent	<i>Adiantum digitatum</i>	
U'	Segments not articulate; leaves erect		V
V	Petiolule of the first acroscopic pinnule of the basal pinna less than 2mm long; distance between the first pinnule and the rachis less than 3mm	<i>Adiantum subvolubile</i>	
V'	Petiolule of the first acroscopic pinnule of the basal pinna more than 2mm long; distance between the first pinnule and the rachis more than 3mm		W
W	Ceraceous yellow glands absent or restricted among the sporangia	<i>Adiantum poiretii</i> var. <i>poiretii</i>	
W'	Ceraceous yellow glands on the abaxial segment surface	<i>Adiantum poiretii</i> var. <i>sulphureum</i>	

A FIELD SURVEY OF *PTERIDIUM AQUILINUM* (DENNSTAEDTIACEAE: PTERIDOPHYTA) MYCORRHIZAS

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ABSTRACT

Roots of *Pteridium aquilinum* were sampled from natural populations in the Northern Hemisphere and routinely found to contain mycorrhizal fungi. Amount of infection varied greatly between sites, but was not correlated with soil moisture, pH, nitrogen or phosphorus content. The significance of these findings in relation to *Pteridium* grown in controlled conditions is discussed.

INTRODUCTION

It is clear that very few plants growing in natural plant communities are free from mycorrhizal infection, and studies which have included pteridophytes indicate that they are no exception (e.g. Lohman 1927; Bouillard 1957). Fungal enhancement of phosphorus (P) uptake has been found to be the main reason for improved growth in infected plants and the uptake of other elements and water may also be important (see Read 1984, for review). Experiments with Southern Hemisphere *Pteridium aquilinum* (L.) Kuhn (subsp. *caudatum* (L.) Bonaparte var. *esculentum* (Forster) Kuhn) have shown that mycotrophic plants grow significantly better than uninfected controls in soils with low P levels (Cooper 1975) and that roots of *Pteridium* growing in New Zealand are consistently mycorrhizal (Cooper 1976). Cooper concluded that the available P in the soil influenced the extent to which roots became mycorrhizal (Cooper 1976). There are reports of *Pteridium aquilinum* (subsp. *aquilinum* var. *aquilinum*) mycorrhizas in Britain (e.g. Conway & Arbuthnot 1949; Hepden 1960) but these refer to very few plants, sites and soil types. *Pteridium* frequently inhabits nutrient-poor soils in Britain but the role played by mycorrhizal infection in the widespread success of this species has never been assessed. The aim of the present study was to investigate the incidence of mycorrhizas in well-established Northern hemisphere *Pteridium* populations and to relate it to soil parameters.

MATERIALS AND METHODS

Twelve well-established *Pteridium* sites were sampled during the summer months: Stiperstones, Shropshire (SO 372976); White Nancy, Bollington, Cheshire (SJ 939772); Winterside Farm, Bollington, Cheshire (SJ 955780); Bakestonedale Moor, Pott Shrigley, Cheshire (SJ 955798); Birch Knoll, Langley, Cheshire (SJ 932722); Ladybower, Bamford, Derbyshire (SK 202855, 217876); Tegsnose Country Park, Langley, Cheshire (SJ 948723); Erwood Hall, Derbyshire (SK 004754); Buddock, Cornwall (SW 786324); Nr. Owslebury, Hampshire (SU 473234); Richmond Park, Surrey (TQ 207742); Nr. Harleston, Norfolk (TM 250835).

Rhizomes and roots were excavated and treated as follows. The dry weight of rhizomes and roots in 1 m x 1 m x 15 cm deep areas were determined and infection levels of sub-samples of roots were estimated. Roots were also excavated from leading edges and central portions of well-established stands. Infection levels were

microscopically assessed in 1cm segments of roots which had been washed, cleared in 10% KOH, acidified and stained in lactophenol blue according to the method of Phillips & Hayman (1970). Roots which could not be processed immediately were fixed in FAA, those which did not clear after several hours at 90°C in KOH were cleared with hydrogen peroxide. Treatment with alkaline hydrogen peroxide (after Phillips & Hayman) failed to clear *Pteridium* roots, but freshly made (acidic) 10 vols solutions of hydrogen peroxide rapidly cleared them. Pilot experiments in which infection was recorded as absence or presence of infection per root segment indicated that this method gave less accurate results than percentage root length infected (after Biermann & Linderman 1981). The latter method was therefore adopted throughout the study: between 40 and 150 segments of root per sample were examined, the percentage length infected estimated, a mean value calculated for each sample and the 95% confidence limits and the standard errors calculated.

Fresh roots from the Cornish sample were also attached to a scanning electron microscope (SEM) slug and plunged into slushed liquid nitrogen inside a Hexland slushing chamber. The chamber was evacuated and the slug transferred to a Cambridge S150 SEM fitted with a (Hexland) stage cooled with nitrogen at -190°C. The roots were sliced open with a cooled blade and transferred into the SEM. The specimens were briefly warmed to -80°C to remove ice, withdrawn into a pre-chamber at -180°C and sputter-coated with gold. The coated roots were then returned to the SEM at -180°C and photographed.

Additional *Pteridium* sites in Switzerland, Spain, Hungary, NE and NW USA were also sampled and analysed for presence and absence of mycorrhizal infection.

Soil samples were taken from around the rhizomes at each site and analysed. Soil pH was measured using the method of Peech (1965). Total nitrogen and phosphorus, and available phosphorus content were measured using the methods of Black *et al.* (1965). Soil moisture content was assessed by oven drying the samples for 18 hours at 105°C and subtracting the dry from the wet weight. Results were adjusted to reflect amounts in grams of dry soil.

RESULTS

Microscopic analysis

The roots of all the specimens examined showed evidence of mycorrhizal infection. The majority of roots contained fungal elements which stained blue with lactophenol blue within the tissues, a small number contained, in addition, limited areas occupied by yellow/brown coloured fungal structures. As the blue-staining mycorrhizal infection was by far the most common and widespread only this will be described in detail.

In heavily infected specimens, a continuous layer occupied by fungi occurred throughout many roots. This layer consisted of a fungal zone, one or two cells deep, immediately outside the stele, e.g. Fig. 1a and b. Infection was never observed within the stele or meristematic tissues, and was never associated with signs of tissue damage or necrosis. The mycorrhizal layer was interrupted at sites of lateral root emergence. Infected cells contained either finely divided arbuscules and hyphae (e.g. Fig. 1c) or coils of coarser hyphae (e.g. Fig. 1d). Some specimens contained thick-walled spherical vesicles throughout the cortex (e.g. Fig. 1e). In roots with low levels of infection, fungal structures were often limited to discrete patches of inner cortex and such limited areas were often connected to a single external hypha. External hyphae were never found to have formed ectomycorrhizal sheaths but penetrated roots directly or, where root hairs were present, by entering the distal part of the hair. Once in the outer cell layers the hyphae branched, giving rise to hyphae which penetrated

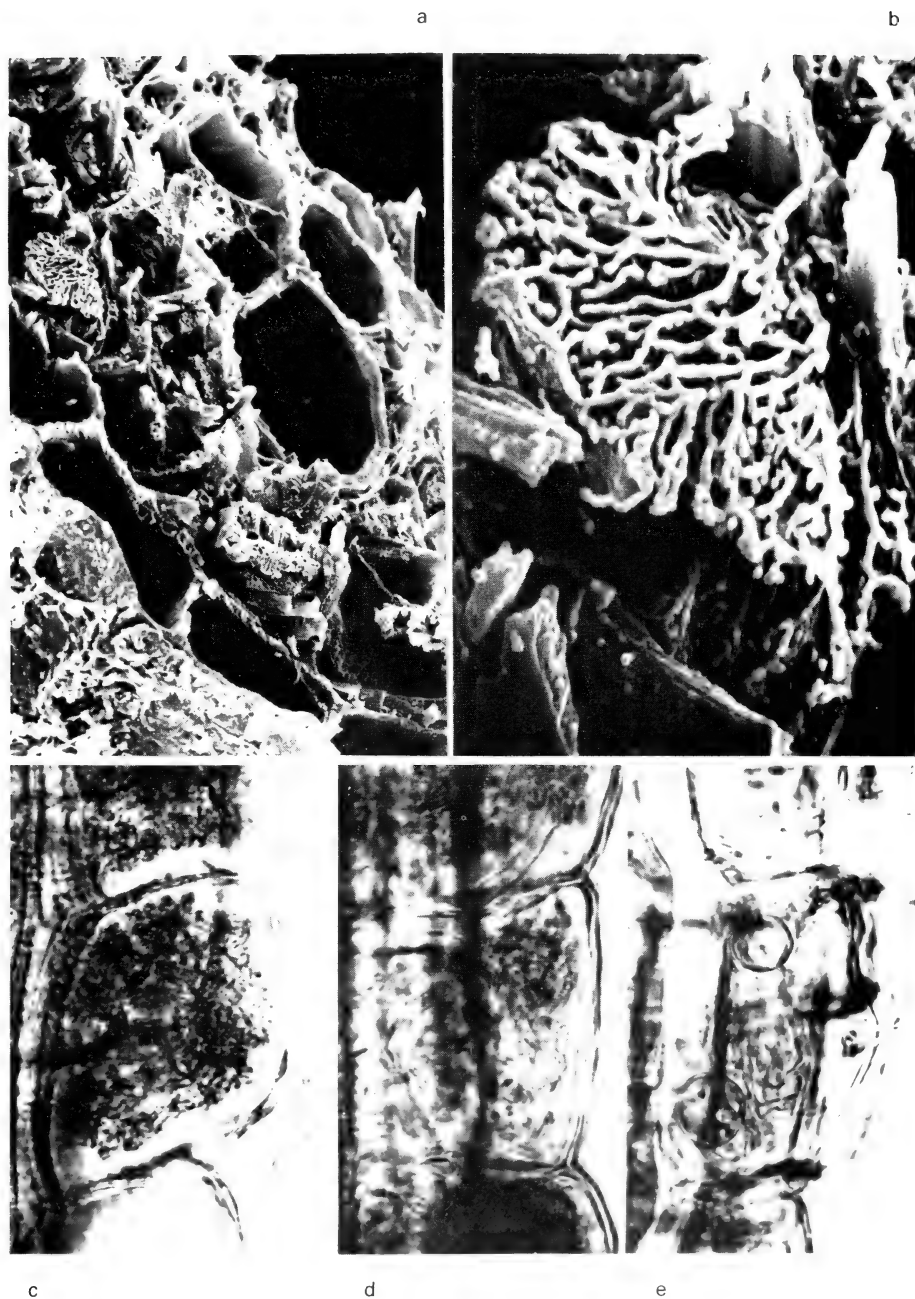


Figure 1. All photo-micrographs show *Pteridium aquilinum* mycorrhizal infection, a) Cryo SEM of fractured root to show cells outside the stele occupied by fungal structures x 100; one cell enlarged in b), x 400. c) - e) Light micrographs of cleared, stained roots. c) Finely divided arbuscule, x 300. d) Hyphal coils, x 300. e) Spherical vesicles and hyphae, x 360.

cortical cells next to the stele. Hyphae also ran through the cortex, parallel to the long axis of the root, and penetrated inner cortical cells to either side of the original point of entry into the root.

Site analysis

Soil moisture ranged from 0.22-3.72g H₂O (g dry soil⁻¹), total nitrogen from 2.09-12.48μmol, total phosphorus from 1.09-5.79μmol, available phosphorus from 0.02-1.81, and soil pH from 2.4-5.3. The infection levels of roots sampled from leading edges of *Pteridium* and those from the centre of well established stands did not differ significantly. Although infection levels differed significantly between sites, the differences were not correlated with differences in soil moisture, total nitrogen, total or available phosphorus content, soil pH, or dry weight of rhizomes and roots m⁻². As phosphorus was thought to be the most important site variable in the present context Fig. 2 is included to illustrate the data relating to available phosphorus and amount of infection.

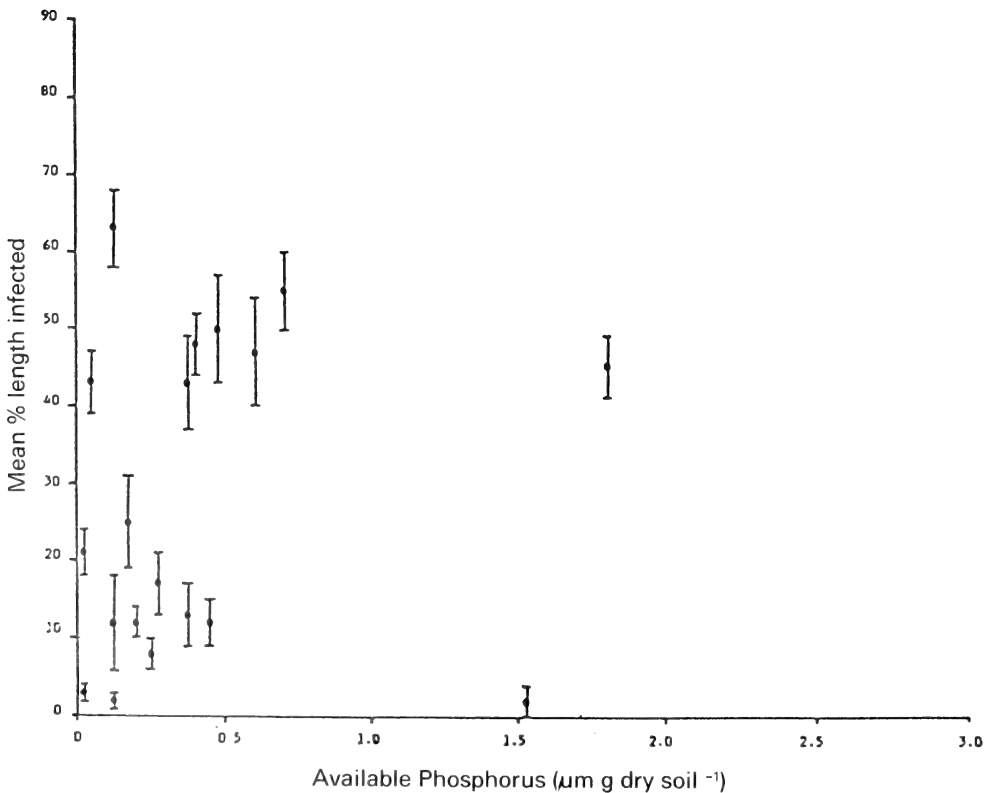


Figure 2. Mean percentage length of mycorrhizal infection in *Pteridium aquilinum* root segments plotted against available phosphorus in soil from nineteen different sites. mean percentage length infected was calculated according to the method of Biermann & Linderman (1981) and bars show the standard error about each mean. Available phosphorus was calculated according to the method of Black *et al.* (1965).

DISCUSSION

The results of the present study do not confirm the contention of Cooper (1976) that the available P in the soil influences the extent to which *Pteridium* roots become mycorrhizal. This lack of agreement is apparent rather than real, however, as Cooper based her statement on the results of uninfected versus infected plants grown in pots of soil with various P levels (Cooper 1975). In these experiments there was a clear influence of P level on percentage infection. In the field Cooper herself reported that root samples from soils relatively high in available P seemed to be no different from the rest (Cooper 1976, see also Hepden 1960). In this respect, therefore, *Pteridium* in the Northern Hemisphere resembles *Pteridium* in the Southern Hemisphere, but the reasons for the difference between experimental and field data are not immediately apparent. From Cooper's (1975) results a lower level of infection would be expected in plants growing in soils of high P. If plants routinely become infected, perhaps even at the prothallial stage, it may be that those growing in poor soils derive more benefit from the association than those in rich soils. Since soil pH, nitrogen, phosphorus and moisture levels are not correlated with infection, the present study provides no indication of factors which determine levels of infection. Higher or lower levels of infection must reflect site parameters untested in this investigation, or individual differences between plants. *Pteridium* in Britain is well known to be highly polymorphic (e.g. for cyanogenesis, Hadfield & Dyer 1986; in DNA composition, Jubrael, Sheffield & Moore 1986; and in morphology, Page 1986) so levels of infection may reflect another inherent polymorphism, perhaps linked with factors which account for variations observed in susceptibility to pathogenic fungal infection (Burge pers. comm.).

Although this study cannot account for the differences found in infection levels it is clear that Northern Hemisphere *Pteridium* is routinely mycorrhizal. This has important implications for studies of mineral nutrition of the fern, and casts a new light on those which have, in the past, been conducted with plants raised from spores in axenic conditions. Where such plants have been cultivated in sterile media (e.g. Schwabe 1951, 1953; Conway & Stephens 1956) they cannot have been mycorrhizal, so the results of these studies, upon which much of the recent work on nutrient cycling has been based, are questionable. Definitive studies of *Pteridium* nutrient cycling clearly require natural, not sterile, conditions, and it seems likely that this applies to most ferns, in view of the large body of data on fern mycorrhizas (e.g. Lohman 1927; Hepden 1960; Bouillard 1957). Fungal symbionts do not seem to have figured in plans to combat the "bracken problem" and it is feasible that *Pteridium* on poor soils would be severely disadvantaged by fungicides. Since experimental plants are known to grow very poorly in the absence of mycorrhizal fungi in soils of low P (Cooper 1975), elimination of the fungal component might provide a new control strategy. Fungicides could be combined with herbicides to provide control in high P soils.

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ADAPTIVE STRATEGIES OF *MARSILEA* (MARSILEACEAE: PTERIDOPHYTA) IN THE LAKE CHAD BASIN OF N.E. NIGERIA

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ABSTRACT

Five species of *Marsilea*: *M. berhautii*, *M. distorta*, *M. minuta*, *M. nubica* and *M. subterranea* occur together near Maiduguri in the Lake Chad Basin of N.E. Nigeria. They differ from one another in their habitat requirements (with regard to water and soil conditions), in their seasonal patterns of growth, reproduction and dormancy, as well as in the position of the sporocarps on the plant and the mode of their protection against adverse external influences. All these characters seem to be of a selective value and apparently originated through an adaptive radiation of sympatric taxa into various ecological niches.

INTRODUCTION

The genus *Marsilea* L. includes c. 50-70 species distributed in the tropical and warm temperate zones of all continents (Cook *et al.* 1974, Gupta 1962, Johnson 1986, Launert 1968, Sadebeck 1902, Tryon & Tryon 1982, Willis 1973). Distinct diversity centres are located in the semi-arid areas of Africa just on the borders of the deserts (Table 1): in the western and eastern parts of Sub-Saharan Africa (10 species and 14 species, respectively), as well as in Southern Africa (16 species) (Launert 1968, 1970, 1971, 1984, Schelpe & Anthony 1986). This unusual diversity apparently originated through an adaptive radiation of sympatric taxa into various ecological niches; an evolutionary process which most probably was stimulated by the extremes of the semi-arid climate, first of all the striking contrasts between life conditions in the rainy and the dry seasons (Kornas 1985).

The aim of the present paper is to illustrate this situation with data collected near Maiduguri in the Lake Chad Basin of N.E. Nigeria, where I had the opportunity to study the vegetation changes during two rainy seasons and the intervening dry season, in 1978 and 1979. The field work was partly sponsored by the University of Maiduguri, Nigeria. The final version of the paper was prepared under a grant of the Polish Academy of Sciences (project MR-II.2.2.4).

The specimens collected are deposited in the Herbarium Universitatis Jagiellonicae Cracoviensis (KRA), with duplicates in Kew (K) and the University of Maiduguri Herbarium.

STUDY AREA

The Lake Chad Basin of N.E. Nigeria is an extremely flat country with almost no local relief (Fig. 1). It occupies the former lake bottom of the Early Holocene, and it is limited in the south by the old shore line (Bama Ridge) at an altitude of c. 330m (Grove 1970). It is covered with a mosaic of recent deposits of the lake and its deltas, ranging from highly impermeable, black, cracking lagoonal clays to sands (Land Systems 1970). The climate of the area is of an extremely hot semi-arid type (tropical climate with summer rains, type II of Walter 1971). The mean annual temperature exceeds 26°C, the absolute maximum temperature reaches above 42°C, and the mean annual rainfall is about 600mm (Fig. 2). There is a short rainy season of c. 4 months (June-September) and a prolonged season of drought of c. 8 months (October-May). The plant cover consists mainly of thorn savannas of various types (Sudanese woodland and wooded grassland of White 1983), most of them being highly degraded by overgrazing and fuel wood collecting.

TABLE 1
The genus *Marsilea* in Africa south of Sahara (Launert 1984).
Species endemic to one centre are in frames.

Western Tropical Africa	Eastern Tropical Africa	Southern Africa
<div> <p><i>M. berhautii</i> Tardieu</p> <p><i>M. minuta</i> L. var. <i>incurva</i> (A. Br.) Launert</p> </div> <div> <p><i>M. gibba</i> A. Br.</p> <p><i>M. minuta</i> L. var. <i>minuta</i></p> <p><i>M. subterranea</i> Lepr. ex A. Br</p> <p><i>M. aegyptiaca</i> Willd.</p> <p><i>M. coromandelina</i> Willd.</p> <p><i>M. distorta</i> A. Br.</p> <p><i>M. nubica</i> A. Br. var. <i>nubica</i></p> <p><i>M. nubica</i> A. Br. var. <i>gymnocarpa</i> (Lepr. ex A. Br.) Launert</p> </div>	<div> <p><i>M. gibba</i></p> <p><i>M. minuta</i> var. <i>minuta</i></p> <p><i>M. subterranea</i></p> <p><i>M. aegyptiaca</i></p> <p><i>M. coromandelina</i></p> <p><i>M. distorta</i></p> <p><i>M. nubica</i> var. <i>nubica</i></p> <p><i>M. nubica</i> var. <i>gymnocarpa</i></p> </div> <div> <p><i>M. aethiopica</i> Launert</p> <p><i>M. botryocarpa</i> F. Ballard</p> <p><i>M. fadeniana</i> Launert</p> <p><i>M. megalomanica</i> Launert</p> </div> <div> <p><i>M. farinosa</i> Launert</p> <p><i>M. macrocarpa</i> C. Presl</p> </div>	<div> <p><i>M. aegyptiaca</i></p> <p><i>M. coromandelina</i></p> <p><i>M. distorta</i></p> <p><i>M. nubica</i> var. <i>nubica</i></p> <p><i>M. nubica</i> var. <i>gymnocarpa</i></p> </div> <div> <p><i>M. farinosa</i></p> <p><i>M. macrocarpa</i></p> </div> <div> <p><i>M. apposita</i> Launert</p> <p><i>M. burchellii</i> A. Br.</p> <p><i>M. capensis</i> A. Br.</p> <p><i>M. ephippiocarpa</i> Alston</p> <p><i>M. fenestrata</i> Launert</p> <p><i>M. schelpiana</i> Launert</p> <p><i>M. unicornis</i> Launert</p> <p><i>M. vera</i> Launert</p> <p><i>M. villifolia</i> Bremek. & Oberm. ex Alston & Schelpe</p> </div>

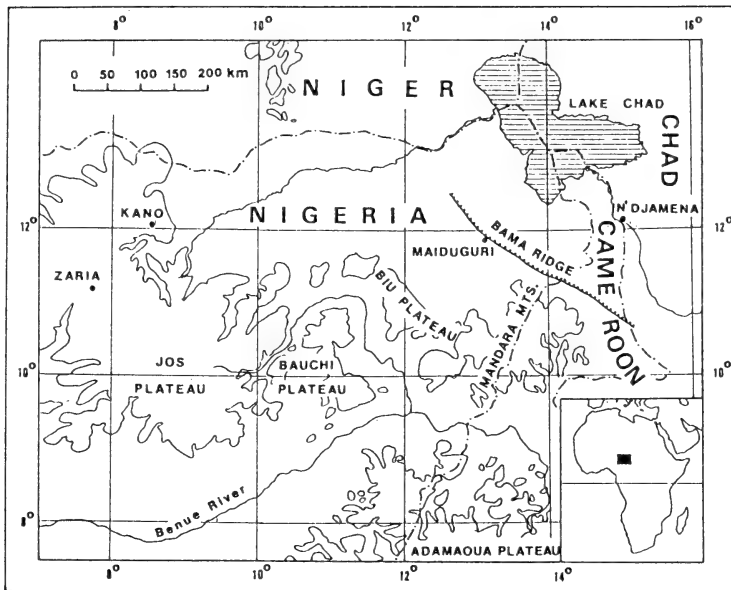


FIGURE 1. Map of North-Eastern Nigeria.

At the end of the rains vast areas of the savanna are covered with innumerable shallow pools, which shrink during the dry season and uncover their muddy bottoms. A rich ephemeral aquatic and amphibious vegetation appears in these pools. It is composed of a variety of short-lived species, either annuals or perennials, with their perennating organs buried in the mud. The angiosperms with deeply hidden corms, *Aponogeton conjugatus* Schum. & Thonn., *Burnatia enneandra* M. Micheli and *Nymphaea micrantha* Guill. & Perr., are good examples of this life-form (the nomenclature of the angiosperms follows Hutchinson & Dalziel 1954-1972).

There is a considerable share of pteridophytes in the flora of seasonal pools in the Lake Chad Basin, including the quillwort *Isoetes schweinfurthii* A. Br. (with perennating corms) and five species of the water fern *Marsilea* (with two kinds of perennating organs: creeping rhizomes and hard, thick-walled sporocarps): *M. berhautii* (Fig. 3), *M. distorta* (Fig. 4), *M. minuta* (Figs. 5, 6), *M. nubica* (Fig. 7) and *M. subterranea* (Fig. 8) (for a complete list of specimens collected see Kornaś 1983). That so many *Marsilea* species are able to coexist in the study area is evidently because they occupy different ecological niches.

ECOLOGICAL SPECIALIZATION IN *MARSILEA*

The *Marsilea* species of the Lake Chad Basin differ remarkably from one another in their habitat requirements (with regard to the water and soil conditions), in their seasonal patterns of growth, reproduction and dormancy, as well as in the location of sporocarps on the plant and the mode of their protection against adverse external influences, especially desiccation. One species, *M. berhautii*, seems to be strictly aquatic, with the rhizomes rooting in the bottom of pools (up to 0.5m deep) and the stems and leaves floating on the water surface (Fig. 3). I did not see terrestrial forms of this species, neither did I find indications of such forms in the literature

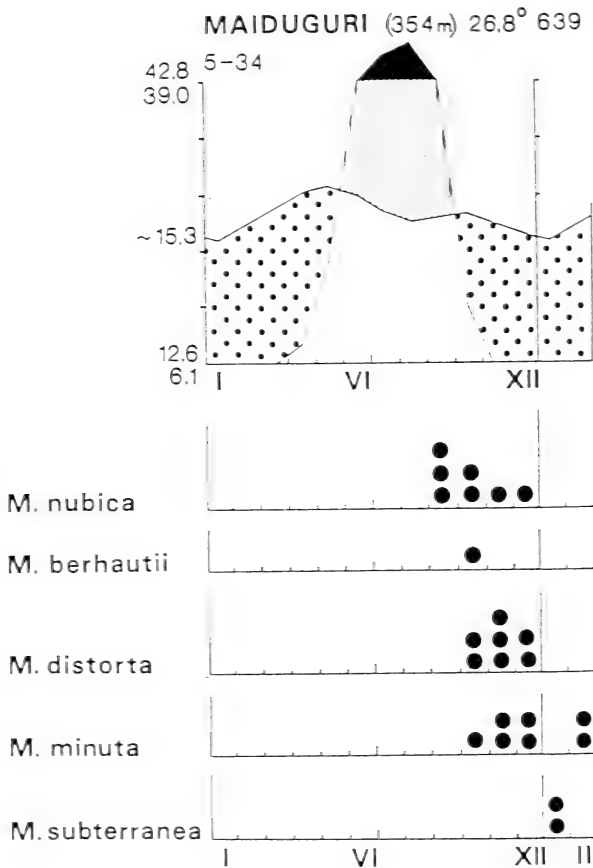


FIGURE 2. Climate diagram of Maiduguri drawn after Walter & Lieth 1960 (above), and phenology of *Marsilea* species in the Lake Chad Basin near Maiduguri in 1978-1979 (below): each dot designates one herbarium collection.

(see Johnson 1986: 13, Launert 1968: 279). On the contrary, *M. distorta* (Fig. 4) appears in pools usually only when they are already completely dry, and thus represents a truly terrestrial plant (see Launert 1968: 285); its aquatic form with submerged rhizomes and floating leaves occurs only exceptionally (I collected it only once, in a pool 5 cm deep). The three remaining species, *M. minuta*, *M. nubica* and *M. subterranea*, are very typical amphiphytes: they start their development submerged in shallow water and finish it completely emerged on dry soil. The first, aquatic, phase of their growth is purely vegetative; the second, terrestrial, phase is reproductive, with a profuse formation of sporocarps (Figs. 5, 6, 7, 8). The transition from the aquatic phase to the terrestrial one is connected with far-reaching changes in the morphology and anatomy of the whole plant, including roots, rhizomes and fronds (as described for various *Marsilea* species e.g. by Allsopp 1954 & 1963, Gaudet 1964, Gluck 1922 & 1936, Goebel 1918, Gopal 1968, Gupta 1962, Sadebeck 1902, Schmidt 1978, White 1966 and others). The main differences between water forms and land forms of *Marsilea* species are indicated in Table 2 and illustrated in Figures 5-7.

TABLE 2

Morphological differences between aquatic and terrestrial plants in amphiphytic *Marsilea* species

	Aquatic plants with floating leaves	Terrestrial plants with aerial leaves
Rhizome internodes	elongated	short
Roots	thick and relatively unbranched	thin and repeatedly branched
Petioles	long and flaccid	short and stiff
Leaflets	large	small
Terminal margins of leaflets	entire	crenulate or serrulate, or superficially to deeply lobed
Reddish streaks on under surface of leaves	often present	absent
Anatomical structure	less highly differentiated	more highly differentiated
Hair-covering on vegetative parts	few or no hairs	copious hairs
Aerenchymatic tissues in roots, rhizomes and petioles	well developed	much less developed
Stomata	only on the upper surface of leaves (epistomatic), not sunken	on both surfaces of leaves (amphistomatic), sunken
Leaf cuticle	thin on the lower surface, thick on the upper surface	thick on both surfaces
Sporocarps	usually absent	usually present

Edaphic requirements of *Marsilea* species in the Lake Chad Basin are clearly differentiated (similarly as e.g. in the Indian species - Gopal 1969). *M. distorta* evidently requires light sandy soils. It seems that only on such soils this truly terrestrial plant is able to bury underground its growing sporocarps, even when the substratum is already dry. Three other species grow on heavy clay, either exclusively (*M. subterranea*) or nearly so (*M. minuta*, *M. nubica*). Such soils usually contain large amounts of organic matter. As demonstrated by Gopal (1969) the organic matter in soil considerably promoted growth in the Indian species of *Marsilea* which he investigated.

The phenological sequence of the five species occurring in the study area is quite distinct (Fig. 2). The most precocious among them is *M. nubica*, in which fully developed sporophytes with sporocarps could already be collected in September before the rains stopped. *M. distorta* was found from the very beginning of the dry season (in October), *M. minuta* a few weeks later (in November), while *M. subterranea* emerged most tardily (in January), when the rains were already over for a couple of months and even the most persistent pools were nearly dry. In places where two species of *Marsilea* occurred side by side, a concentric zonation was noticed, with the more precocious species on the periphery and the tardier one in the centre of the pool (Fig. 9). Under such circumstances the outer species may already appear in its land form and pass through its second, reproductive phase, with plenty of sporocarps, while the central one still remains in the first, vegetative phase and displays the features of a typical water form. A similar zonation was noticed by Johnson (1986: 26, 41) in a drying pond in northwestern Venezuela, where *M. ancylopoda* A. Br. grew in the emerged outer zone, and *M. deflexa* A. Br. in the central submerged one.

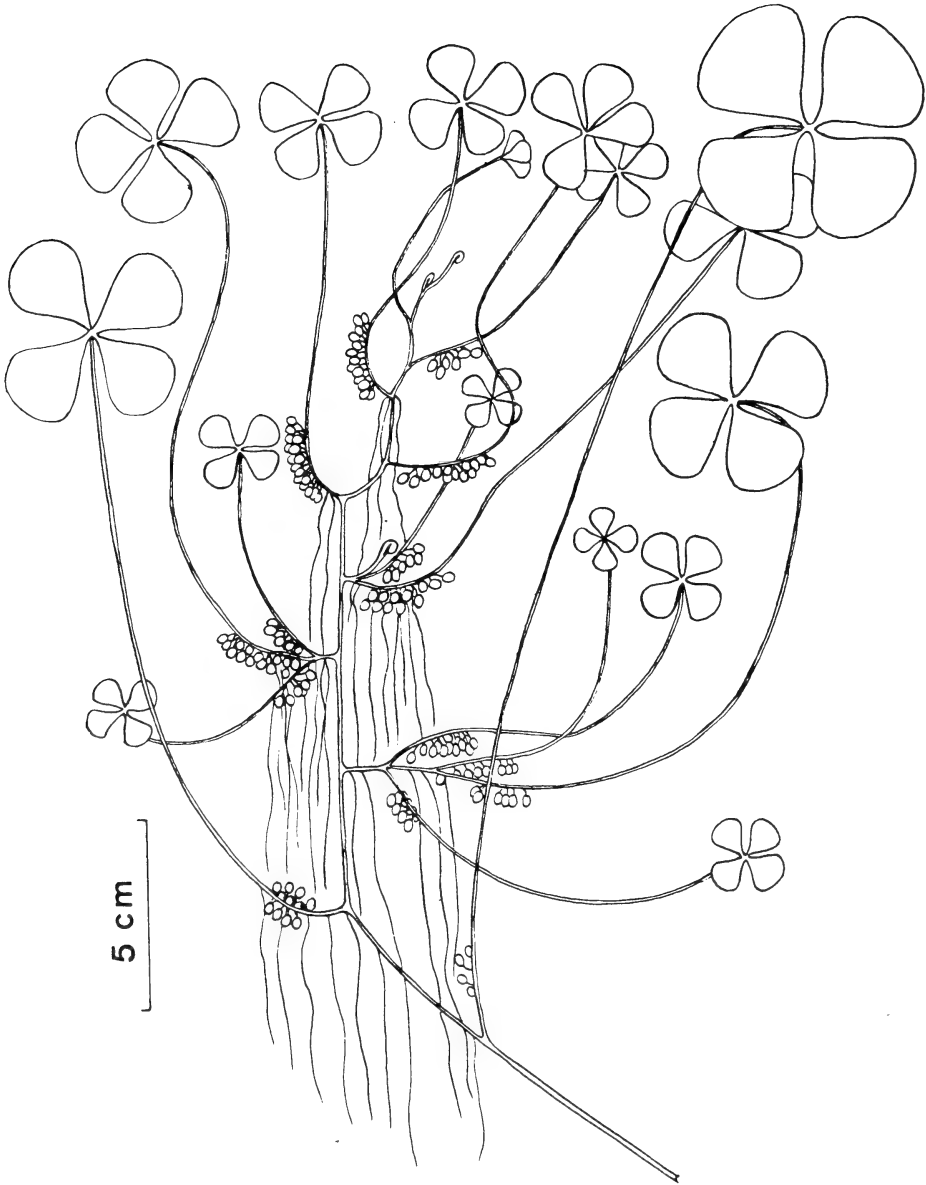


FIGURE 3. *Marsilea berthautii*: aquatic species with floating shoots and freely exposed sporocarps. 27 October 1977, J. Kornaš Pl. Afr. 6282, KRA.

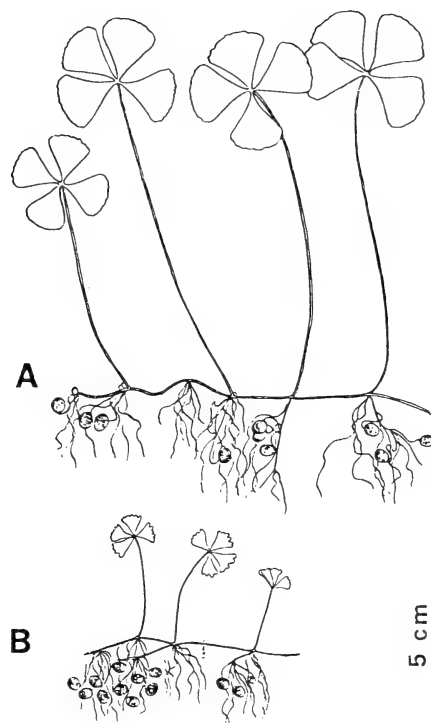


FIGURE 4. *Marsilea distorta*: terrestrial species with geocarpic sporocarps. Plants appearing earlier in the dry season (A) are rather mesomorphic, while those appearing later (B) have more xeromorphic features. A - 26 October 1977, J. Kornaš Pl. Afr. 6271, KRA; B - 2 December 1977, J. Kornaš Pl. Afr. 6433, KRA.

The position of sporocarps on the plant not only forms an essential taxonomic character of the *Marsilea* species, but it is also of a great biological importance for them. In *M. berhautii*, the only truly aquatic species, the sporocarps are produced in long rows high on the petiole and thus fully exposed, without any kind of protection (Fig. 3). Two of the amphibious species are basicarpic, with sessile (*M. nubica*) or shortly pedicellate (*M. minuta*) sporocarps attached to the base of the petiole, just above ground level (Figs. 6, 7). The third amphibious species, *M. subterranea*, is geocarpic, with sporocarps buried underground due to the positive geotropic growth of pedicels, which penetrate the clay to a depth of 1 cm or more when it is still water-logged and soft (Fig. 8). The only terrestrial species under investigations, *M. distorta*, is also geocarpic (Fig. 4). Both basicarpy and especially geocarpy result in the location of sporocarps in the immediate vicinity of the parent plant (atelechory), and seriously impede their long-distance dispersal (telechory) which occurs in *Marsilea* through the activity of water birds (Johnson 1986, Malome & Proctor 1965). As pointed out by Stopp (1958), atelechoric dispersal (which never occurs in true aquatics) is known mainly in plants of arid and semi-arid zones. It results in the offspring being placed in the same ecological niches in which their parents occur, i.e. under suitable

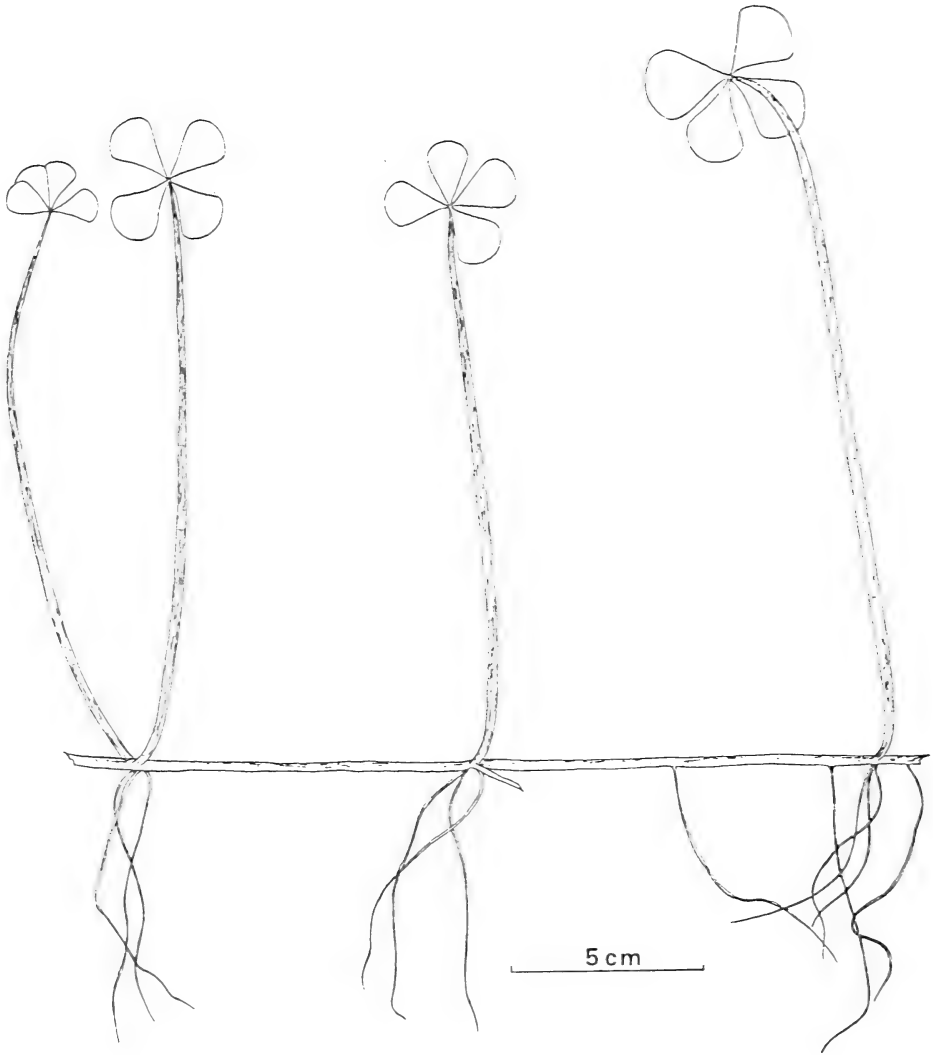


FIGURE 5. *Marsilea minuta*: sterile aquatic plant with floating leaves. 16 November 1977, J. Kornaš Pl. Afr. 6378, KRA.

habitat conditions. This is of course of special importance in the extremely patchy environment of the arid and semi-arid zones, where small strictly localized pockets with favourable life conditions (pools in the case of *Marsilea*) are surrounded by vast expanses of hostile dry land.

It is tempting to hypothesize that in the evolutionary history of the genus *Marsilea* in Africa there was a shift in the pedicel attachment resulting in the switch from an exposed position of sporocarps in the ancestral hydrophilous species to the basicarpic

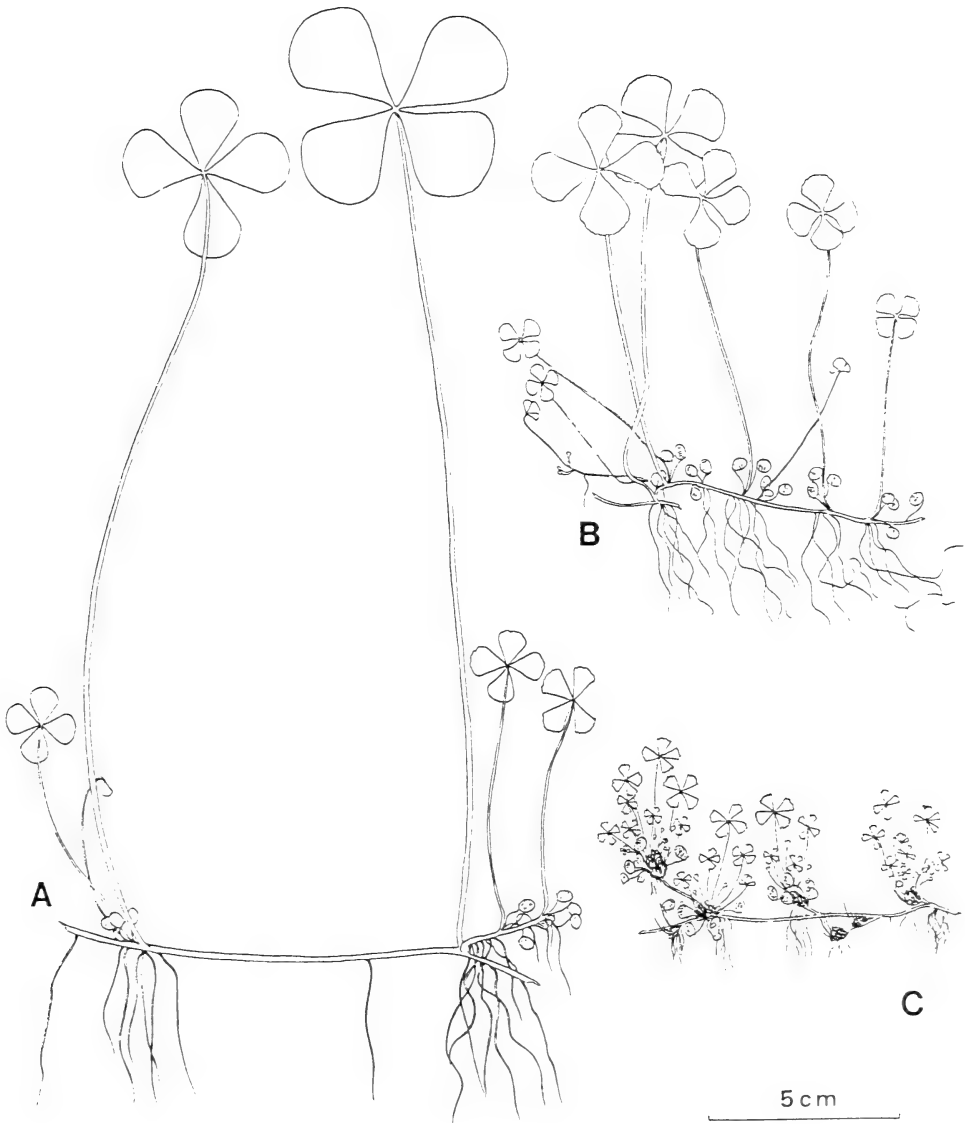


FIGURE 6. *Marsilea minuta*: fertile plants with basicarpic sporocarps. A - transitional stage between aquatic and terrestrial forms with both floating and aerial leaves: B, C - terrestrial plants changing from mesomorphic to xeromorphic features as the drought increases. A - 16 November 1977, J. Kornaš Pl. Afr. 6378, KRA; B - 24 November 1977, J. Kornaš Pl. Afr. 6418, KRA; C - 3 February 1978, J. Kornaš Pl. Afr. 6626, KRA.

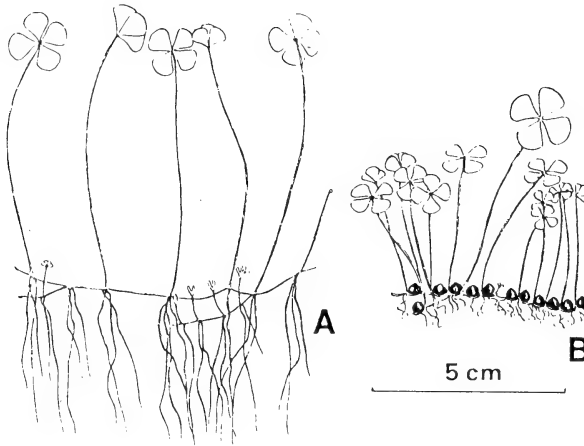


FIGURE 7. *Marsilea nubica*: amphibious species with basicarpic sporocarps. A – sterile, aquatic plant with both submerged and floating leaves; B – fertile terrestrial plant. A – 30 September 1977, J. Kornaš Pl. Afr. 6161, KRA; B – 16 November 1977, J. Kornaš Pl. Afr. 6379, KRA.

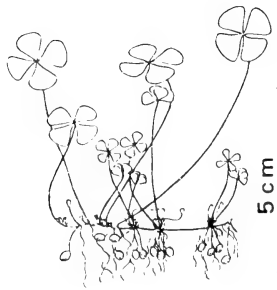


FIGURE 8. *Marsilea subterranea*: amphibious species with geocarpic sporocarps. 19 January 1978, J. Kornaš Pl. Afr. 6581, KRA.

and geocarpic position in the derived xerophytic species, with simultaneous restriction of the long-distance (telechoric) dispersal in favour of the atelechoric one. The conclusions of Bhardwaja's (1967, 1980) and Gopal's (1968) studies on the Indian species of *Marsilea* are quite consistent with this hypothesis. It fits very well in a more general hypothesis of Johnson (1986: 14) that in *Marsilea* "adaptations toward passing a greater portion of the life on land are secondarily acquired, rather than primitive, being superposed on a plant form and life cycle designed for life in water".

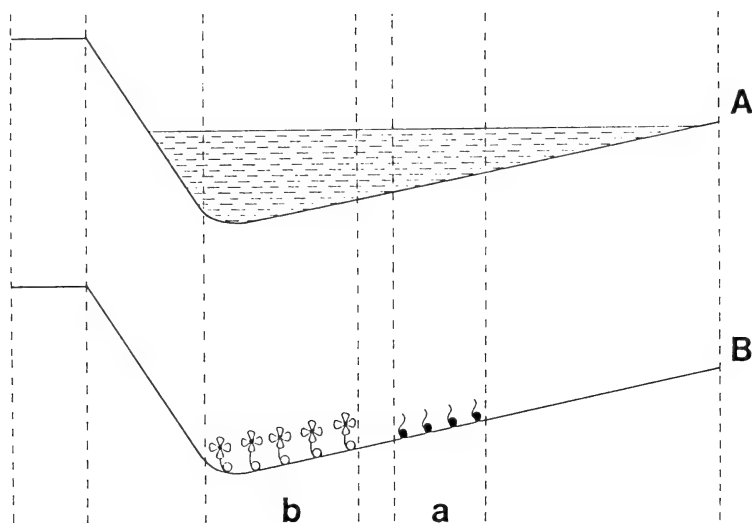


FIGURE 9. Zonation of *Marsilea* species in a roadside ditch near Gajibo on Maiduguri - Gambaru road. A - pool filled with water at the end of the rainy season; B - dried out pool late in the rains (3 February 1979): a - *M. nubica* (leafless and completely dry), b. - *M. minuta* (with small living leaves).

AN OUTLOOK

There are possibly many more biological features of the *Marsilea* species in the arid and semi-arid zones which contribute to the success of these plants in their harsh environment, and certainly deserve a closer study. One of such peculiarities is the notorious longevity of sporocarps, which are reported to be able to germinate after more than 60 or even 100 years (Allsopp 1952, Bhardwaja 1980, Bloom 1955, Johnson 1985, Stopp 1958), and their extreme resistance against environmental stress (drought, heat, etc. - Bloom 1961). Another is the hygrochastic mechanism of sporocarp dehiscence, connected with the ability of the gametophyte of an immediate fertilization and a rapid development of young embryos in the aquatic medium (Johnson 1986: 25). Still another peculiar feature is the production of drought-resistant vegetative propagules ("tubers" consisting of condensed rhizome branches with many small leaves), reported to occur not only in the Australian species *M. hirsuta* R. Br. (Braun 1873, Goebel 1918, Clifford & Constantine 1980), but also in *M. minuta* (Bhardwaja 1980, Gopal 1966, Loyal & Kumar 1979), though not confirmed in the present study. Bizarre growth forms in some African species, e.g. in *M. botryocarpa* (Launert 1968, 1984) or *M. megalomanica* (Launert 1970, 1984) suggest that still more unknown life-phenomena may be discovered in this fascinating and biologically little explored genus.

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SHORT NOTES

***DRYOPTERIS VILLARII* (DRYOPTERIDACEAE: PTERIDOPHYTA) A NEW HIGH-MOUNTAIN SPECIES IN THE CARPATHIANS**

In 1986, when collecting field data for the "Atlas of distribution of the vascular plants in the Tatra National Park" (Western Carpathians, Poland) we found one plant of a fern unknown to us. As this was in very late October, after the first ground frosts in the mountains, the plant was badly damaged and with no spores on it. In this state certain identification was not possible. Next year, 1987, very careful field searching in the same region resulted in finding three more specimens, this time in very good condition. Their gross morphology (Fig. 1), the dense indumentum of glandular hairs on both sides of fronds and some other features indicate that they belong to *Dryopteris villarii* (Bellardi) Woyнар ex Schinz & Thell. subsp. *villarii*.

The locality is in the Polish part of the Tatra Mts, in the postglacial hanging valley called "Swistowka Wielka" above the "Wantule" strict reserve (upper part of the Dolina Mietusia valley), at an altitude of 1360m, in the *Pinus mugo* (subalpine) belt (considerably lowered in this region because of orographic conditions). The species occurs there on limestone block scree of fairly large boulder size, in an open situation, on a slightly (5°) inclined northern slope. The rather moist soil, consisting of mineral grains intimately mixed with well-decomposed black humus, develops there in local pockets among boulders. The very small population of *D. villarii* (only three plants on about one square metre) was accompanied by the following species: *Aconitum variegatum*, *Allium montanum*, *Asplenium viride*, *Bellidiastrum michelii*, *Carduus glaucus*, *Carex sempervirens*, *Delphinium oxysepalum*, *Galium anisophyllum*, *Poa alpina*, *Rhodiola rosea*, *Saussurea alpina*, *Saxifraga aizoides*, *S. moschata*, *S. paniculata*, *Scabiosa lucida*, *Selaginella selaginoides*, *Solidago alpestris*, *Thalictrum minus*, and *Viola biflora*.

The locality of *D. villarii* in the Tatra Mts is the first site not only for Poland and for this part of Europe, but also for the Carpathian Mts as a whole. The nearest known stands of this species in the Eastern Alps (Fraser-Jenkins 1977, Fraser-Jenkins & Reichstein 1984) are about 500km distant from the locality discovered.

The authors are greatly indebted to Dr W.H. Paryski for improving the English style of the manuscript.

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Fig. 1. Fronds of *Dryopteris villarii* subsp. *villarii* from the locality in the Tatras.

LYGODIUM JAPONICUM IN SINGAPORE

Holttum (Flora Malesiana II, 1(1), 1959) says *Lygodium japonicum* (Thunb.) Sw. is native only to regions with a pronounced dry season, and Alston & Holttum (Reinwardtia 5, 1959) reported that it will grow in cultivation in Singapore but not vigorously, and that in its natural habitat the fronds probably die out during the dry season, to appear again with the beginning of the wet period.

For the last five years or more *L. japonicum* has apparently been growing profusely around the periphery of the lawn as well as along the fence fronting a house occupied

for years by expatriate Japanese at Chun Tin Road, Singapore. These plants are evergreen and fertile most of the time, encouraged presumably by the wet climate.

We are grateful to Professor R.E. Holttum of The Royal Botanic Gardens, Kew for confirming the identification of our specimen.

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DRYOPTERIS X GOMERICA (*DRYOPTERIDACEAE: PTERIDOPHYTA*), NEW FOR EUROPE

THE DISCOVERY

In September 1986 the author, A.C. Jermy (BM) and M. Hermy (INC, Hasselt, Belgium) met Prof. M. Mayor-Lopez and H. Nava (Oviedo) for a reconnaissance trip in Asturias, N. Spain, to prepare an excursion-guide for the XIVth International Botanical Congress in Berlin (Viane, Mayor-Lopez & Jermy 1987). Asturias was chosen since it is particularly rich in pteridophytes (c. 66 taxa), with arctic-middle european (c. 30%), atlantic (c. 26%), mediterranean (c. 23%), macaronesian (c. 13%) and endemic (c. 5%) taxa (see also Fraser-Jenkins & Gibby 1986). The wet and mild climate on the Mirador del Fito (600m alt.) in the Sueve Mts., north of Arriondas and only c.4km from the Gulf of Biscay supports a mixture of most interesting ferns, including *Culcita macrocarpa* C. Presl (Fraser-Jenkins & Lainz 1983). The acid, greyish-white sandstone is covered with *Ulex gallii* - *Erica arborea* - *E. mackaiana* heathland and some isolated groups of *Betula*, *Pinus* (planted) and *Eucalyptus* (planted). This site is probably the only locality in northern Spain where both *Dryopteris aemula* (Ait.) O. Kuntze and *D. guanchica* Gibby & Jermy grow together abundantly. It was here, at the base of some large boulders and well protected against grazing by an almost impenetrable spiny mass of *Ulex*, that a large plant, intermediate in morphology between *D. aemula* and *D. guanchica*, was collected (R. Viane 3355). Part of the rhizome was taken for cultivation and subsequent cytological study. Closer observations, showing that the plant has aborted spores and that micromorphological characters are also intermediate between *D. aemula* and *D. guanchica*, led us to identify the plant as *D. x gomerica*. Fixations for cytological analysis were taken in May 1987 and sent to H. Rasbach (Glottertal, W. Germany) who reported (in litt. 27.9.1987 & 11.11.1987) that the plant is triploid with $n = c. 41^{II}$ and 41^I at meiosis. This result not only confirms our identification but is also in agreement with the results of Gibby & Widén (1983).

Hitherto *D. x gomerica* was only known from La Gomera (Canary Isl.), apparently the only other locality where both parents grow together. Unlike the Azores, the Canary Islands (and Madeira) are *not* included in the area covered by the Flora Europaea, thus our new Asturian locality is the first record for mainland Europe.

THE DISTINCTION

Cytological, chemical and morphological evidence have led to the present interpretation of the relationships between *D. x gomerica* and its parents (Gibby *et al.* 1978; Gibby 1979; Gibby 1983; Gibby & Widén 1983). *D. guanchica* is an allotetraploid species that originated via chromosome doubling of a hybrid between *D. intermedia* ssp. *maderensis* and *D. aemula*. *D. x gomerica* thus represents a "backcross" of *D. guanchica* with its *D. aemula* ancestor (fig. 1); consequently the overall morphological distinction

between these taxa is fading out through the morphologically intermediate hybrid (fig. 1).

Some characters for identification are given in the table below. All values are in μm ; they represent the mean \pm the standard deviation; "glands" means the unicellular capitate hairs, "hair" means all uniseriate multicellular hairs.

Abbreviations used (hairs): Lt = total length; Lc = length apical cells; Wc = width apical cells; N = number of cells in a hair. For the glands: Lt = 3 total length; dA = diameter of apex; dB = diameter of base; ls = stalk length.

MACROSCOPIC CHARACTERS

	<i>D. aemula</i>	<i>D. x gomerica</i>	<i>D. guanchica</i>
plant habit	fronds: flat, drooping	fronds: erect	fronds: erect
frond colour	medium to yellow-green	yellow-green	blue(metallic) to dark green (N.Spain)
pinna	flat with drooping tip	flat	flat (occas. convex when pinnules reflexed)
pinnules	concave: edges and whole ultimate segment turned up	flat with only the edge of the segment and its ultimate tip turned up	flat, rarely slightly convex, but with the extreme segment tip turned up
pinna apex	attenuate to caudate	caudate	caudate

MICROSCOPIC CHARACTERS

	<i>D. aemula</i>	<i>D. x gomerica</i>	<i>D. guanchica</i>
cytology	diploid: $n = 41^{\text{II}}$	triploid: $n = 41^{\text{II}}$ & 41^{I}	allotetraploid: $n = 82^{\text{II}}$
spores	good	aborted clumps	good
exospore	$34 \pm 2 \mu\text{m}$ long		$34 \pm 2 \mu\text{m}$ long
perispore	costate-venate	irregular	(narrowly) costate-echinulate
sori	with paraphyses = laminal hairs	no paraphyses	no paraphyses
sporangia	2-cellular gland-tipped hair or unicellular gland at the base	glabrous, rarely with a gland	glabrous, rarely with a gland
indusium			
dorsal	glandular or glabrous	glands	glands
marginal	glands and (often) hairs	glands and hairs	glands only
stomata	$39\text{-}44\text{-}49 \mu\text{m}$ long	$45\text{-}48\text{-}52 \mu\text{m}$ long	$44\text{-}49\text{-}54 \mu\text{m}$ long
		lamina indument	
small paleae	slightly bullate with \pm isodiametric cells and a long uniseriate apex	intermediate	not bullate, cells elongate
hairs:			
Lt	210 - 360 - 510	450 - 660 - 750	250 - 450 - 700
Lc	30 - 50	37 - 57	36 - 54
Wc	18 - 28	34 - 36	31 - 45
Lt/Wc	1.3 - 2.1	1.5 - 1.9	1.1 - 1.5
N	7 - 13	9 - 15	8 - 14
glands:			
lt	53 ± 7	73 ± 6	76 ± 8
dA	43 ± 5	48 ± 3	38 ± 5
dB	15 ± 2	17 ± 1	18 ± 2
ls	17 ± 5	25 ± 6	36 ± 8
dA/ls	2.7	1.9	1.1
dA/dB	2.9	2.8	2.1

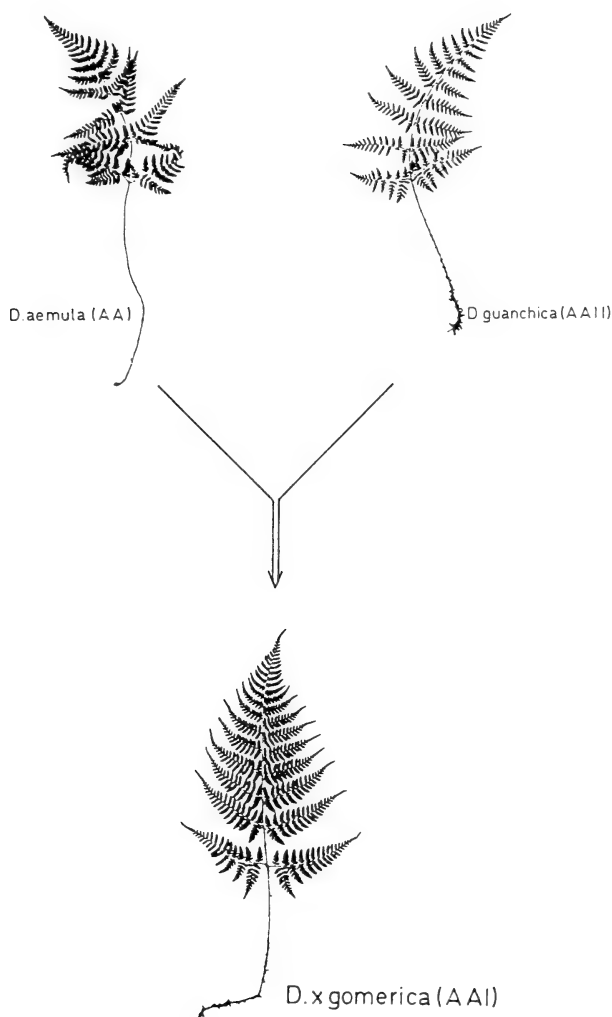


FIG. 1 Silhouettes of *Dryopteris x gomerica* and its ancestors.

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REVIEWS

LIEBMANN'S MEXICAN FERNS by J.T. Mickel, R. McVaugh, S. Karell and H. Balslev. 350 pp. *Contributions from the New York Botanical Garden* volume 19. 1987. ISBN 0 89327 324 4. Price \$30.50 for U.S. orders, \$31.75 for non-U.S. orders.

Liebmann's Mexican Ferns consists of an Introduction by John Mickel, an Itinerary and Gazetteer by Rogers McVaugh, a translation of Liebmann's "Mexicos Bregner" by Sven Karell and Henrik Balslev, an index to the translation, a reprinting of Liebmann's "Mexicos Bregner" (in Danish) and an index to "Mexicos Bregner". Liebmann's "Mexicos Bregner" has for a long time been inaccessible to the average botanist both on account of its rarity as a publication - it is only held in major botanical libraries - and because although the plant descriptions are in Latin the important field observations and comments are in Danish. It is a work of great importance to students of Mexican ferns, being the second of the four Mexican fern floras produced last century. Like the first of these floras (Martens & Galeotti, *Mémoire sur les Fougères du Mexique*, 1842), Liebmann's work (1849) was based on field experience in Mexico, unlike the two later works (Fée, *Catalogue méthodique des fougères et des Lycopodiacees du Mexique*, 1857 and Fournier, *Mexicanas plantas*. Vol. 1. *Cryptogamia*, 1872) which were prepared in Paris and based only on herbarium collections. Liebmann provided information on 308 species, 95 of which were described as new.

The authors are to be congratulated upon making Liebmann's work more widely available both by translating it and reprinting the original. The addition of modern names and synonymy to the translation makes it usable with the modern fern floras available for some Mexican states while the itinerary and gazetteer will be of great use to students of Liebmann's collections, whether of ferns or higher plants.

B.S. PARRIS

FERNS OF MALAYSIA IN COLOUR by A.G. Piggott. 458 pp. Tropical Press, Malaysia. ISBN 967 73 0029 6. 1988. Price £43.00, U.S. \$69.00 including surface mail postage or M\$150.00.

This beautiful book is the product of many years work by Audrey Piggott and her husband John who took the photographs. It is intended as a companion volume to *Flora of Malaya Volume II Ferns of Malaya* by Dr R.E. Holttum (1954 and 2nd edition 1968), and, in spite of its rather misleading title which led to a colleague purchasing the book under the misapprehension that he would be able to identify East Malaysian (Sabah and Sarawak) ferns, its coverage is effectively that of Peninsular Malaysia and Singapore, i.e. that of Holttum's original work. The addition of *Phanerosorus*, a genus which occurs in East Malaysia but not in the Peninsula, I find irrelevant as numerous other fern genera with a similar distribution could well have been included but would have lessened the book's value as a companion to *Ferns of Malaya*. In fact many of the species illustrated here also occur in Sabah and Sarawak although their occurrence in either or both of these states is only mentioned for six taxa.

The format consists of an introduction, a summary of the life cycle of a fern, the principal vegetation types and fern habitats, pests and diseases of ferns and the main account of the ferns which are arranged in a taxonomic order based partly on Holttum, partly on *Flora Malesiana* revisions and partly on Pichi Sermolli's generic arrangement. With two exceptions, *Monachosorum* and *Polystichum*, all fern genera currently known to occur in Peninsular Malaysia are included in Piggott's book. Of the 598 fern taxa in the area (Parris, unpublished data) 392, or c. 66%, are illustrated. The discrepancy between this figure and the nearly 80% coverage claimed by Mrs Piggott is largely due to numerous very recent revisions and additions to the flora which have appeared since the book went to press, judging by the date of April 1984 at the end of the acknowledgements. These include Bidin, *Fern Gazette* 12: 360-361, 1984 (*Osmunda vachellii*), Croxall, *Kew Bull.* 41:519-531, 1986 (new records of *Microgonium* (= *Trichomanes* p.p. of Piggott and Holttum), Holttum, *Gardens' Bull.* 38:145-148, 1985 (two new species of *Tectaria*) and Parris, *Kew Bull.* 41:491-517, 1986 (new species and new records of Grammitidaceae). Surprisingly one species described in this last paper has found its way into the book, however.

The name used in Holttum and the page number where the species is described are given for easy reference. Where the currently accepted name is different from that in Holttum, the name he used is also given, although no distinction is made between taxonomic synonyms and misidentifications by Holttum which should correctly be cited as '*sensu* Holttum' rather than being attributed to their authors. The nomenclature is on the whole up to date with that used in revisions available at the time of writing although, inexplicably, three names in *Lindsaea* have not been brought up to date with those used by Kramer in his account of the genus for *Flora Malesiana* although others have been corrected. *Lindsaea scandens* should be *L. parasitica*. *L. nitida* should be *L. integra* and *L. decomposita* should be *L. cultrata*. Other incorrect names used are *Trichomanes proliferum* for *T. minutum*, *Asplenium squamulatum* for *A. vittaeforme*, *A. adiantoides* for *A. polyodon*, *Tectaria oligophylla* for *T. fissa* and *Blechnum indicum* for *B. serrulatum*.

For almost every taxon included there is a habitat photograph, a photograph of a frond and a close-up photograph showing details of the frond which usually includes the sori, together with distribution notes, a short description and medicinal uses where known. The photographs are of good quality on the whole and show various diagnostic features. The inclusion of traditional medicinal uses adds to the interest of the book. Many scientists are now concerned with recording such information and testing the

efficacy of 'bush medicines' and this compilation will doubtless be a useful aid to ethnobotanists working in the peninsula.

Our state of knowledge of the fern flora of the Malaysian Peninsula is far from complete, as shown by the number of taxa discovered in or described from the area since this book was written. I am preparing descriptions of another three new species from the peninsula (one *Coryphopteris* and two *Grammitis*); the first was collected by me during field work in 1986 and is not represented otherwise by herbarium specimens while the other two have been known and wrongly identified in herbaria for several years. There are probably many more such additions to be made to the flora both by field work and by detailed studies on existing herbarium specimens, but they will not detract essentially from the usefulness of Holttum's classic work on Malayan ferns, which remains one of the best fern floras ever written, or from Piggott's book which with its colour photographs and nomenclature updated to c. 1983 will be a good companion volume. I would recommend this book, in fact, to everyone who has a 'Holttum' and an interest in ferns in this part of the world.

B.S. PARRIS

OBITUARY

IRENE MANTON (1904-1988)

Emeritus Professor Irene Manton, F.R.S., for thirty years an honorary member, and past-President (1969-1972), of the British Pteridological Society, died in hospital in Leeds on 31 May 1988, after a brief illness.

The younger of two eminent biologist daughters of a London dentist, Irene Manton was educated at St. Paul's Girls' School, and at Girton College, Cambridge, where she undertook both undergraduate (1923-6) and postgraduate (1926-9) studies. She had become fascinated with chromosomes whilst still at school, and the opportunity to indulge her interest came when she spent the first year of her postgraduate research in Stockholm in 1926-27. Her early work was on the cytology of the Cruciferae and she came to a study of ferns almost accidentally, through a happy combination of her passion for chromosomes and her appointment in 1929 to an assistant lectureship in the Botany Department of Manchester University where the then Professor of Cryptogamic Botany, W.H. Lang (himself trained by the famous pteridologist, F.O. Bower, and discoverer with Kidston of the early fossil pteridophyte genus, *Rhynia*), was using *Osmunda* in experimental studies on the effect of induced apogamy on the cytological basis of alternation of generations. She studied the cytology of Lang's apogamously produced plants and in the process discovered not only another polyploid series (she had found her first in the watercress) but also the delights and technical tractability of the Osmundaceae as cytological subjects. This led to her series of important papers on the spiral structure of the chromosomes in the Royal Fern, *Osmunda regalis*. Other ferns, however, were not so easy, and proved to be such difficult cytological material that she immediately determined to conquer them. During the war years she worked tirelessly on the British pteridophyte flora and, when the war came to an end, she had accumulated so much data that she decided to publish her results in book form, *Problems of Cytology and Evolution in the Pteridophyta* (1950). She had by this time moved to Leeds, having been appointed to the Chair of Botany in January 1946, and it was here that she took up her next challenge. The recently invented electron microscope, by the great increase in resolution which it provided, had opened up boundless possibilities for the microscopist, and Manton responded by setting up the first, which was for some time the only, laboratory in the world to study the ultrastructure of plants. Electron microscopy, with which she was to be principally involved for the whole of the rest of her life, became her new consuming passion, while the fern work was continued by her colleagues, research students and visiting postdoctoral research fellows. She was an exacting, and at times intimidating, person to work for, as she had high standards and did not tolerate fools gladly: on occasions we all felt the rough edge of her tongue. But we knew also the other side: her warm, affectionate nature, her extreme kindness and generosity to those of her 'family' in need and her well-developed sense of fun. She had a vigorous intellectual curiosity, and throughout her life she retained a child's infectious delight in the thrill of making discoveries. She had a quick, incisive mind, great energy, an enormous capacity for hard work as well as boundless enthusiasm. Her research was her life, and she cared little for such things as food, clothes and holidays. Botany House during the 1960's was an exciting place to be. As professor she was busy during the working day with her teaching duties and with administration, but every evening and weekend she worked on her electron microscope. There was a wonderful atmosphere of active research that permeated the department, and her colleagues and students were stimulated to work similar ungodly hours. Indeed, we felt guilty about taking an hour off on Saturday afternoons to buy food for Sunday's lunch!

However, it was not only botanical research to which she devoted her abilities. Sometimes, during the evening, she would take a break for coffee, and such occasions were an opportunity for her to show us, with characteristic delight and pride, her latest acquisition, whether it was a fragment of papyrus text, a piece of Roman glassware or a new painting. Her life-long interest in form and shape led her far beyond the bounds of science and into the world of art. She was an avid collector of artifacts, prints and paintings which she bought as they took her interest, and not at all for their intrinsic value. These were used to illustrate lectures and talks and especially to, stimulate the young, (her own expression). A naturally gifted person, who, in addition to her other skills, was a talented violinist, she appears, from a very early age, to have had a keen sense of history, particularly as it applies to biology (an early article, written whilst still a student, describes the history of the vine, and is illustrated by motifs from Greek pottery), and she was able to weave art and science together in a novel and entertaining manner. She also had a highly original way of viewing life and one of her most stimulating series of lectures was entitled 'Other Ways of Looking at Nature', which was illustrated by reproductions of cave paintings as well as by modern abstract and by Chinese art. A natural story-teller, she held her lecture-audiences spell-bound from beginning to end. Her innumerable scientific papers are written in the same inimitable, racy style. In 1969 she retired from the Chair of Botany at the University of Leeds and, with characteristic determination and energy, embarked on what was to be another nineteen years of active and fruitful research. 'Life begins at 65' well describes her retirement, which included major expeditions to Greenland and the Galapagos Islands in order to collect her beloved nanoplankton.

Irene Manton had a long association with the British Pteridological Society which she joined in 1936. In the summer of 1938 she went on their Annual excursion to Kenda. Having already discovered different chromosome numbers in the fern *Lastrea* (= *Dryopteris*) *filix-mas*, she was hoping to find wild material of 'var. *abbreviata* (DC) Newman' so that she could count its chromosomes, and participants at the meeting were able to advise her where she could find it. It is interesting to note that generations of Manton's research students, raw at the outset of their postgraduate studies, have since followed the same path, similarly having been guided to either plants or localities by the kindness and field experience of Society members. Manton's early investigations on hybrid *Dryopteris* in Britain are published in the Gazette of December 1938, and the continuation of this work and her extension of it to the rest of the British fern flora, culminating in the publication of her book in 1950, have already been mentioned. Preliminary data from the island of Maderia, also included in the book, laid the foundation for the comparative cytological analysis of fern floras in different parts of the world while the extension of the investigation to the tropics began in late 1950 with the Leeds University Botany Department's expedition to Ceylon, where some 70% of its fern flora was cytologically sampled during the course of this one visit; as in the temperate floras already examined, evidence of evolution through polyploidy and hybridization was revealed. In Ceylon too Manton first met Professor R. E. Holttum of Singapore and their subsequent friendship and collaboration led not only to her study of the chromosomes of Malayan pteridophytes and to the use of chromosome numbers in tracing fern phylogeny but also to the successful application of cytogenetic methods to various groups of tropical ferns. Finally, her pioneering work utilising the pairing behaviour of the chromosomes in hybrids to unravel the evolution of and the relationship between species in polyploid complexes has been taken up and used extensively in the elucidation of difficult groups in the fern floras of Europe, North America and Australasia. Manton's own lively description of how

her involvement with ferns came about (her Presidential Address to the Society in October, 1972) is published in two parts in *Gazettes* 10 (6), 1973 and 10 (7), 1974 while numbers 10 (2), 1969 and 10 (3), 1970, issued to commemorate her retirement from the Chair of Botany at Leeds in 1969, carry articles by her colleagues and former research students. Lovis (*Gazette* 10 (1), 1968) details the methods originally devised by Manton for the hybridization of ferns, whilst her own last note for the *Gazette* (13 (3), 1987) records her friendship and collaboration with Professor T. Reichstein of Basel, an association which has resulted in the successful cytogenetic analysis of virtually all the European ferns.

As a scientist, Irene Manton's great strengths were the ability to see the potential in a new method or instrument, and the development and adaptation of it to suit her own material or interests. A recurring theme throughout her life was her exploitation of new techniques. Having in her early cytological research used laborious nineteenth-century methods of staining and sectioning, she was quick to realise the importance of the acetocarmine squash technique (combined with the McClintock method for making slides permanent). Both of these she applied very successfully to fern chromosomes, and was able to establish reliable counts, even in high polyploids, for the first time. Later on, the use of snail cytase to break down cell-walls enabled root-tip squashes to be routinely made and analysed. She also developed photographic methods for recording her results and never returned to the drawings with which she started at the outset of her career. She was one of the earliest microscopists to exploit for biological purposes the increased optical resolution available through the use of the ultra-violet microscope, and the enthusiasm with which she took up electron microscopy at the earliest possible opportunity is a story too well-known to be reiterated here.

Her remarkable career was recognized by her election to Fellowship of the Royal Society (1961) and to the Presidency of the Linnean Society (1973-76) as well as to honorary membership of various scientific societies on both sides of the Atlantic. She has been awarded honorary doctorates from the universities of McGill (1958), Oslo (1961), Durham (1966), Lancaster (1979) and Leeds (1986) and is the holder of numerous prizes and medals for her work.

It has been a privilege to have known her personally and to have worked under her supervision, and her many colleagues and friends will, while they mourn her passing with sadness, remember her with great affection.

ANNE SLEEP

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THE FERN GAZETTE

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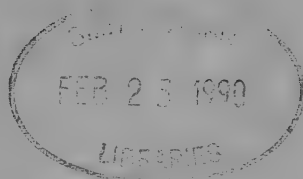
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THE
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THE HISTORY OF *DIPHASIASTRUM ISSLERI* (LYCOPODIACEAE) IN BRITAIN AND A REVIEW OF ITS TAXONOMIC STATUS*

A.C. JERMY

British Museum (Natural History), Cromwell Road, London SW7 5BD

ABSTRACT

The history and distribution in Britain of the plant known today as *Diphasiastrum issleri* is reviewed. In the past there has been much confusion over its identity and relationship to *D. alpinum* and *D. complanatum*. The diagnostic characters are described and taxonomic relationships reconsidered. It is proposed because of apparent introgression between the taxa and the likely hybrid origin of *D. issleri*, that it and *D. alpinum* be regarded as subspecies of *D. complanatum* and the necessary new nomenclatural combinations are made.

HISTORY

A taxon distinct from the common alpine clubmoss (*Diphasiastrum (Lycopodium) alpinum*) was first recognised as a British plant (as *Lycopodium complanatum* L.) in an editorial note in the *Gardeners' Chronicle* for 11 August, 1866 (p. 753) reporting a communication from John Lloyd, claiming "it was found by a woman named Sarah Young, while occupied in cutting Heath for broom-making", at Lower Waggoner's Wells, Bramshott, Hants. It was presumably this record that Charles Cardale Babington (1867) refers to in edition 6 of his *Manual of British Botany*, adding "I have not seen it, and doubt its being correctly named". However, a year later John Lloyd sent specimens to the editor of the *Gardeners' Chronicle* (Lloyd 1867a) labelled *Lycopodium alpinum*, from Bramshott, "where the soil is a sandy peat, the elevation not more than 600 or 700 feet, the situation sheltered, growing near the roots of Heath about 18 inches high, by which it appears to be almost smothered". An editorial comment followed this, saying its exact identity is not certain as the specimen was sterile and that Professor Babington "inclined to place it under *L. chamaecyparissus* A.Br." (a taxon described from N. America and also found in Europe, very closely related to *L. complanatum* and regarded as synonymous with it at that time). Lloyd commented that the main creeping stem was beneath the soil and believed that *L. alpinum* produced stems above the soil. However, in the *Chronicle* seven weeks later he wrote (Lloyd 1867b) that he found *L. alpinum* with subterranean stems in Wales and therefore believed this character not to be important. In edition 7 of the *Manual*, Babington (1874) still referred to the plant as *L. complanatum* but it is omitted entirely from the 8th edition (Babington 1881). Later, in a four-page *Addendum* to the *Manual* Babington (1883) had obviously reconsidered his opinion and cites *L. complanatum* from Hants., Gloucester, Worcester, Ross and Skye. Watson (1870) also recorded the Bramshott plant as *L. complanatum* but also gave "Worcestershire (?), error (?) Bab. Man., ed. 6, p. 445. Leeft msc." According to Druce (1882) C.C. Babington wrote to him saying the Rev. Churchill Babington found "in July, 1838, on Hartlebury Common, Worcestershire, a *Lycopodium* which he thought might be *L. complanatum* or *chamaecyparissus* but of late considered to be only a form of *L. alpinum*, growing at a rather low situation". Babington did not mention a Miss Lea (later Mrs Waller), who accompanied him that day, and that she also collected a specimen of the *Lycopodium* (Lees 1867). Her herbarium has not been located (cf. Kent & Allen 1984), but a sterile scrap of a specimen from Hartlebury is in CGE, however, and appears to be *D. issleri*.

The next and possibly most significant find was by the Rev. Henry Peter Reader who in 1881 collected in Woodchester Park, near Stroud, Gloucs., a plant he thought was *L. alpinum*. A specimen, which had very flattened suberect branches and cones on short

* This paper was originally submitted for Part 3 dedicated to Professor Doctor TADEUS REICHSTEIN whose prolific studies on European ferns are a stimulus to many, including the author.

peduncles, was sent via Bolton King to Druce, who was stimulated to publish (Druce, 1882) a note "On *Lycopodium complanatum* as a British plant"

The Gloucestershire plant was lent by Druce to Boswell-Syme who had a drawing made of it by N.E. Brown for *English Botany* (Boswell-Syme 1886). The Plate is labelled *Lycopodium alpinum* L. var. *decipiens*, Boswell "believing the plant to have nothing to do with *L. complanatum*" (in litt. to Druce, 3 June 1883). It is numbered 1834* and obviously is meant to be bound next to 1834 (*L. alpinum*); no description was given in the text by Boswell-Syme. Druce rectified this in a valid publication (1892) distinguishing it from *L. alpinum* "by its larger size, by its flattened spreading branches, with central leaves on the flattened stem more erect than the lateral", giving "Scotland, Westmoreland, Cumberland, Gloster and Worcester" as localities. Tab. 1834* of Boswell-Syme is referred to and hence the type is Reader's plant from Woodchester. Specimens were distributed widely by Father Reader; that in BM is designated here as **lectotype** with **isolectotypes** seen from BRIST, CGE, K and OXF. They all possess cones although mostly over-mature, but are a very good match for continental *D. issleri*. Edward Marshall compared the Woodchester plant with material labelled *L. complanatum* in the Linnean herbarium and published (1891) an opinion that Reader's plant "must go under *L. alpinum* L." and "*L. complanatum* ought to disappear from our list"; this is understandable, the plant is much closer to *alpinum*.

As for other material recorded as *L. complanatum* (or *L. alpinum* var. *decipiens*), Babington (1883) referred also to Skye and Ross. The Skye plant was collected by Prof. Marmaduke Alexander Lawson and H.E. Fox in 1868 and was exhibited at the Linnean Society on 22 November 1885 by J.G. Baker. A comment in the *Gardeners' Chronicle* (Anon. 1886) states that "minds have been set at rest by the fine specimen of this species [*L. complanatum*] from the Somerset side of Exmoor", again exhibited by J.G. Baker at the Linnean Society on 17 December, 1885. Both are potentially *D. issleri* (v.i.). Other specimens from Scotland, including ones collected by William Gardner on the Sidlaw Hills, and by Druce and E.S. Marshall in N. Scotland (e.g. Ben Avon, Banff, v.-c. 94, and Lochnagar, c. 3000 ft [1000m], v.-c. 92) were subsequently labelled var. *decipiens*, as were many more at that period; all have proved to be etiolated forms of *D. alpinum*. Similarly the specimen collected near Advie, Grantown-on-Spey, J.S. Gamble, 1871 (K) is recorded by McCallum Webster (1978) as var. *decipiens*. All those specimens seen are sterile and are luxuriant or etiolated forms (through being in dense herbage) of *D. alpinum* (see below), although the Lochnagar material (and site) warrants further investigation. Druce (1916) after summarising the history of *L. complanatum* s.l. and its appearance in Britain, also recorded the closely related species *Lycopodium chamaecyparissus* A.Br. from Ingleborough. The specimen on which that record is based, at Manchester Museum (MANCH), is *D. alpinum*, but on the same sheet is a good specimen of *L. chamaecyparissus* (= *D. complanatum* subsp. *chamaecyparissus* (A. Br. ex Mutel) Kukk.) obviously misplaced in mounting and a suspected source of the error.

TAXONOMIC CONCEPTS OF *L. COMPLANATUM* COMPLEX

It is clear from what has been said above that the status of the names to be applied to these records was by no means clear-cut, even if differences were distinct. Those botanists who looked beyond our shores realised there were other taxa in Europe and North America which might be overlooked. Sir Joseph Dalton Hooker (1884) was one who did not go into such problems in depth; he regarded *L. alpinum* and *L. complanatum* as subspecies – a plausible view – and placed the Gloucester and Worcester plants in ssp. *complanatum*. The status was even reduced further in Bentham & Hooker (1887) where it is dismissed as a form "of warmer climates". As development and change of land-use destroyed lowland heaths of Britain, the true identity of these clubmosses became an academic study.

Early 20th century botanists in Europe reviewed the group from time to time for selected



FIGURE 1. Lectotype specimens of *Lycopodium alpinum* race *issleri* Rouy in Issler's Herbarium (BASBG). (Photo: Botanisches Institut der Universität, Basel.)

areas but their work did not impinge on the British scene. Then, during the 1950's, a Belgian botanist, Dr André Lawalrée, looked at those forms which were intermediate between *L. alpinum* and *L. complanatum*, initially in the Low Countries. He described (1957) as a species, *L. issleri* (Rouy) Lawalrée based on the *L. alpinum* variety (actually "Race") described by Rouy (1913) from material collected by E. Issler in the Vosges mountains, Alsace. Figure 1 shows a sheet from the Issler Herbarium, now at the Botanisches Institut Basel (BASBG). Lawalrée spread his interest to identifying material in British herbaria, and around that time his determinations were sent up by vice-county recorders to BSBI *Proceedings*. Lawalrée's determinations included specimens from Llyn Idwal (in BM, NMW and OXF), already listed by Druce as *L. a.* var. *decipiens*, as *L. issleri*, and this was taken up by Harrison (in Hyde, Wade & Harrison 1969). Lawalrée's concept unfortunately included etiolated specimens of *D. alpinum*, and those from Wales, in the opinion of this author, were that species.

Following this account, Joan Wilce, when a student at Michigan University, looked at the 'Complanata Section' of *Lycopodium* (later to be segregated and accepted as a genus, *Diphasiastrum*) for a Ph.D. project. She suggested (1965) that *L. issleri* was a hybrid, mainly on grounds of partial spore abortion, with *L. alpinum* as one parent and a member of the *L. complanatum* group as the other. This work stimulated more local appraisals in Europe, and two are substantial and worthy of mention here.

First is that of Ilka Kukkonen (1967) who, based in Finland, orientated his work on northern and central European material and did not discuss the *D. issleri* problem to any great extent. Nevertheless his discussion of the characters of the *D. complanatum* complex is pertinent as is his account of hybridity within the complex and the ecology of the species in Finland.

The second publication on this group is by Anna Pacyna (1972a, b) who studied Polish material, including 15 specimens of *D. issleri*. Her biometrical and statistical account is substantial and she concludes that "*D. issleri* ought to be considered a species of hybrid origin". It is interesting that although *D. complanatum* is a common plant in the lowlands throughout Poland and seldom encountered in the mountains, and then very rarely to 1200m altitude, *D. issleri* is recorded in the same altitudinal zone as *D. alpinum* (700 to 1200 or rarely 1600 m).

I have found signs of spore abortion in both the Gloucester specimens and that recently found in the Malvern Hills and have hitherto treated the taxon as a hybrid (e.g. in Jermy *et al.* 1978), whilst accepting that fertile spores are formed and can establish new populations where conditions are suitable. However, as *D. complanatum sensu stricto* has never been proven for Britain it seems unlikely that the hybrid has been formed *de novo*. In view of the fact that *issleri* is intermediate between *alpinum* and *complanatum* and that partly fertile hybrids appear to occur, the opinion of Domin (1937), that these taxa should be treated as subspecies, has a lot of merit. Furthermore, Kukkonen (1967, 1984) presented good evidence for this concept in other European taxa of the complex. I therefore propose that they are accepted at that rank in the British List (synonymy for Europe in Derrick, Jermy & Paul 1987) as follows:

Diphasiastrum complanatum (L.) J. Holub, Preslia 47: 108 (1975) subsp. *complanatum*,
Type: Herb. Linn. 1257. 20 (LINN).

D. complanatum subsp. *issleri* (Rouy) Jermy **comb. nov.**

Basionym: *Lycopodium alpinum* L. race *issleri* Rouy, Fl. France 14:489 (1913).
Lectotype: France, Vosges Mts, on the central ridge between the pass and the Reisberg, on granite, 1298m, E. Issler, 13 Aug 1908 (BASBG).

D. complanatum subsp. *alpinum* (L.) Jermy **comb. nov.**

Basionym: *Lycopodium alpinum* L., Sp.Pl.: 1104 (1753).
Type: Herb. Linn. 1257.15, Lapponia (LINN).

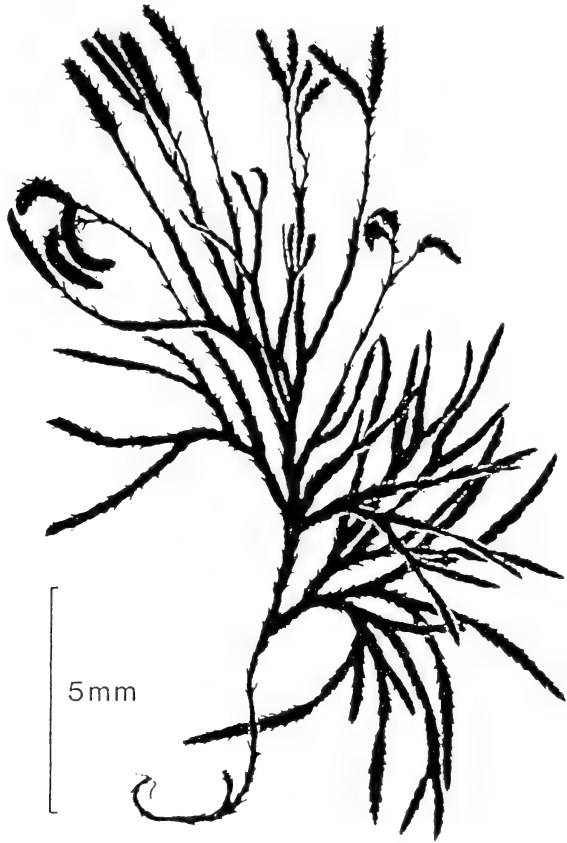


FIGURE 2. Silhouette of *Diphasiastrum complanatum* subsp. *issleri* from Canisp, West Sutherland. (A.G. Kenneth, 1985, BM).

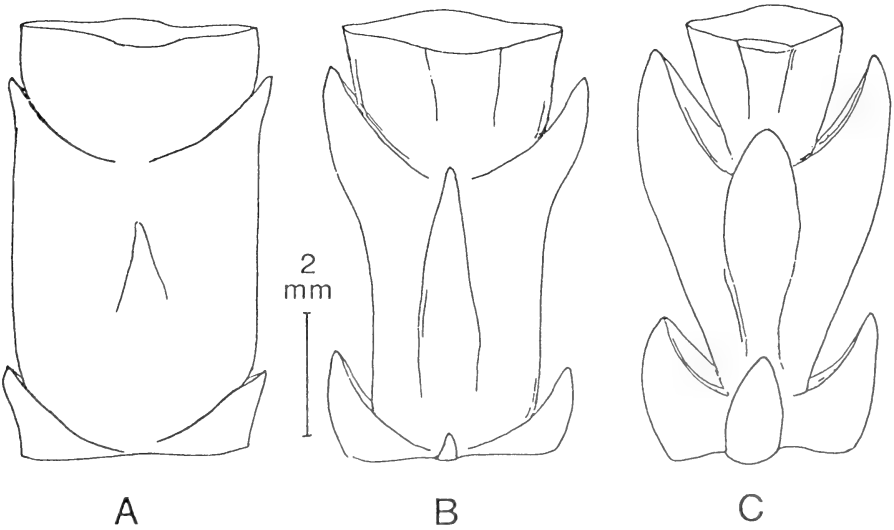


FIGURE 3. *Diphasiastrum complanatum* leaves from second-year-old branches, seen from below. A. subsp. *complanatum* B. subsp. *issleri*. C. subsp. *alpinum*.

IDENTIFICATION OF *DIPHASIASTRUM COMPLANATUM* SUBSP. *ISSLERI*

The morphology of *issleri* is intermediate between *alpinum* and *complanatum*. If the plants are fruiting then the elongated peduncles of the often branched strobilus are distinctive, as is the more open, flabellate sterile branch pattern, with the branch angle quite wide. The compressed appearance of the lower leafy branch of *complanatum* is seen in *issleri*; in *alpinum* the leaves are laxer and the branch appears more terete. Dostal (1984) illustrates this well for European material, and Page (1982) gives a figure of the Gloucester plant; a silhouette of the Canisp material is given in Fig. 2. In *alpinum* the alternate branches tend to lie in one plane, but in *issleri* the branches leave the main stem more or less in a whorled arrangement, giving a rigid look which, with a somewhat more grass- or yellow-green colour (i.e. less glaucous) makes the plant stand out in the community.

Dostal (1984) also gives the spore size for *complanatum* (30-38 μm); that for *alpinum* is 42-47 μm . D. Tennant sent material of the Canisp plant to R.H. Roberts who on measuring the spores found them closer to *alpinum* (mean 41.8 μm ; Tennant, pers. comm.), comparing well with the author's measurements of the Woodchester plant. It is interesting that Roberts found the spores of an untypical form of *alpinum* (sent to him also by Tennant, v.i.) from about 300m above Kenneth's site, to be even smaller (mean 35 μm). On other morphological characters those plants fall within the variation of that species.

The shape of the sporophyll in the three taxa can be seen to be subtly different. In *complanatum* it is very broadly ovate, almost orbicular with an apiculate tip; in *alpinum* it is more narrowly ovate with an attenuate tip; in *issleri* it is intermediate. However, there is considerable variation throughout the length of the cone, and because most material found is sterile, I prefer to emphasise the vegetative characters.

The shape and size of the leaves on branches of the previous year's growth, are the best characters to consider when one is presented with a few branchlets only. Those leaves facing to the ground (so-called ventral leaves) on *complanatum* are narrowly subulate-triangular, adpressed to the stem for most of their length; those of *alpinum* are lanceolate-ovate, with an obtuse apex, or more often trowel-shaped (trullate) with a thick petiole forming the right-angle of the trowel handle so that the leaf stands away from, and with the blade parallel to, the stem, although on drying or pressing, the blade is often characteristically skewed; and those of *issleri* are intermediate in shape, being in British material narrowly triangular with an acute apex and lacking the angled petiolate base.

The shape of the lateral leaves on these older stems is a useful character and has not been commented on before, and is in my opinion very helpful in diagnosing *issleri*. In *complanatum* (Fig. 3A) the keel of the leaf descends parallel to the stem and is abruptly rounded as it approaches the leaf below. The leaf of *alpinum* (Fig. 3C) rapidly narrows to the base, forming a slender 'waist', when seen from the flattened sides, just above the insertion of the next lower pair of leaves; *issleri* (Fig. 3B) shows the intermediate state, the keel not being parallel, but truncate below, rounding abruptly to the stem. Also in *complanatum* the free portion of the lateral leaf is about one third (or even less) of the lower fused base; in *alpinum* the free portion may be almost half the total length. In British *issleri* the free portion is approximately one third.

Branches of *alpinum* when growing in deep litter (or in dense *Cladonia* lichen turf) often become etiolated and appear flattened as in *complanatum*. Such forms have been referred to the latter species in error in British records and herbaria. Close examination shows the ventral leaf to be trullate and petiolate, and the distinct taper to the narrow waist even more obvious.

RECORDS OF *D. COMPLANATUM* SUBSP. *ISSLERI*

The most recent records published of this taxon (as *D. x issleri*) are by Jermy et al. (1978). In the light of this recent reassessment the distribution shown there must be revised. Whatever

its taxonomic status, this taxon is very rare in the British Isles and should not be collected except to verify its identity if field observation and photography prove inadequate. The distribution of *issleri* clearly falls into two categories: a lowland south and eastern England ecotype of which the Woodchester plant is clearly the best example. Other records are based on small samples of plants in herbaria (except for the Broad Down, Malvern, plant) but are, in my opinion, this ecotype. The second category is the Scottish low mountain populations, directly comparable to the Continental material and associated with areas of ancient pine forest. Records of doubtful identity are given in square brackets.

ENGLAND AND WALES

[V.-cs 4/5 **North Devon/S. Somerset:** Specimens from "Exmoor" in BM with no date or collector are sterile but possibly this taxon and may be the gathering reported in the *Gardeners' Chronicle* (Anon. 1886) as being similar to Professor Lawson's Skye plant. A scrappy specimen from "near Lynton" (W.R. Lawson, Dec. 1885) in BM may be the same gathering and may also be *issleri*. Typical *alpinum* has also been recorded from the area however. No post-1930 records of either taxa have been established].

V.-c. 12 **North Hants.:** Lower Waggoner's Wells, Bramshott, specimen comm. C.C. Babington in BM and CGE. The plant has not been recorded there this century but much heath remained into the beginning of this century and indeed broom-making from the heather continued well into the 1930's. Earlier this century Bramshott Common was grazed by cattle and this (or the increased nitrogen) would not have improved the chances of the clubmoss.

V.-c. 34 **West Glos.:** near Woodchester, Stroud, H.P. Reader, several specimens collected over the years 1881-1884 in BM, BRIST, CGE, GL, K, LIV, NMW and OXF. "Gloucestershire" but no locality given (but presumably from near Woodchester) coll. ? Evans, 10 July 1885 (E).

Reader, whose activity played a significant part in Gloucestershire botany whilst he was incumbent at Woodchester found the specimen in "one of the many valleys which intersect the Cotswolds about Stroud, where the ground is broken up into several ferny knolls, divided by streamlets". Upon the side of one of those knolls was the *Lycopodium*. The oolite disappears at that point "leaving the lias exposed, or but thinly and partially covered by a strip of Fuller's Earth". "In consequence", Reader says in a letter to Druce, "the flora of this little tract (some six acres in extent), differs widely from that of the surrounding country and includes a large number of plants which ... are not found, or found but rarely, on the Cotswolds". He mentions a number of species including *Lycopodium clavatum*, *Oreopteris limbosperma*, *Calamagrostis epigeios*, *Carex pallescens*, *C. pilulifera*, *Gnaphalium sylvaticum* and *Vaccinium myrtillus*, the mosses *Plagiothecium denticulatum*, *Pleurozia schreberi* and *Polytrichum juniperinum*, and the lichens *Baeomyces rufus*, *Cladonia cervicornis* and *C. digitata*. As far as I can discover, Reader at no time recorded the exact locality but an annotation in Augustus Ley's copy of Babington's *Manual* in BM quotes Woodchester Park, and the geology suggests the south or east sides of Brown Hill. Extensive searching by the author and Sonia Holland (BSBI Recorder for Gloucestershire) has failed to produce either the plant or a likely habitat.

V.-c. 37 **Worcester:** Hartlebury Common, Kidderminster, Churchill Babington, July 1837 (discussed above), specimen in CGE, not apparently refound, nor collected since.

[Great Malvern, Worcestershire Beacon. August 1893, Freeman-Roper (Amphlett & Rea, 1909 sub *L. alpinum*). Exact locality not known and no herbarium material has been seen.]

[Little Malvern, Herefordshire Beacon, W.W. Boucher, 20 Sept 1934. (Rea annot. in Amphlett & Rea). In 1980 John Day (pers. comm.) discovered a *Diphasiastrum* in same area (on Broad Down) at 250m alt., in heathland referable to the association Calluno-Deschampsietum where *Calluna* and *Deschampsia flexuosa* are co-dominant with *Potentilla*

erecta and *Vaccinium myrtillus* common. Frequent in the area, but as yet not closely associated with the clubmoss, are *Sorbus aucuparia* and *Betula* seedlings and *Pteridium*. The low herb turf contains occasional *Galium saxatile* and *Luzula multiflora* with the following cryptogams: *Campylopus fragilis*, *C. introflexus*, *Cladonia arbuscula*, *C. ciliata* var. *tenuis*, *C. floerkiana*, *C. chlorophaea*, *Dicranum scoparium* and *Pleurozium schreberi*.

The site is being monitored by the Nature Conservancy Council and the Worcestershire Naturalists' Trust (N. King pers. comm.) and the encroaching birch controlled, with full cooperation of the owners, the Malvern Hills Conservators. In November 1986, one plant of *Diphasiastrum* was removed in a turf, so as to keep the rhizosphere intact, and transplanted in a nearby site protected from sheep grazing, but not unfortunately from rabbits, the effects of which were considerable. No trace of the plant could be found in the Spring of 1988. I initially determined this as *D × issleri* (i.e. *D. complanatum* subsp. *issleri*) but in the light of further experience must regard it as a population of subsp. *alpinum* which in the past has hybridized with subsp. *issleri*. It is morphologically half way between *issleri* and *alpinum*: it has the leaf structure of the former, and the branching, colour and shorter cone peduncle of the latter. Such populations should not be unexpected. The taxon *issleri* is most certainly of hybrid origin (v.s.) but the balance of genes (and therefore characters) will not always be identical, and populations will drift towards one or other parent.]

SCOTLAND

V.-c. 88 Mid Perth: Glen Lochy, Allt dubh Ghalair, 975 m. alt., amongst long heather, 29 July 1890, E.S. Marshall (BM, CGE, SLBI). Same locality and collector, 21 July 1906 (NMW).

V.-c. 92 South Aberdeen: Glen Derry, near Braemar, 26 July 1896, F.J. Hanbury (BM); there are remnants of ancient pine forests in this valley and the site could have *issleri* still present.

Strath Nethy, across track to Bynack Beg, in open moorland, between 750 and 800m alt., August 1981, D.J. Tennant (E); this is a small sterile branch but a good match for the taxon.

Lochnagar, on the S.E. slopes at 960 m alt., in short heather c. 7-8 ins high, 1961/62, L. Bentley (comm. F. Rose) (BM).

Glen Quoich, on eastern slopes of A' Chioch, Beinn a' Bhuid, at c. 700 m alt; amongst and beneath dwarf heath of *Calluna-Vaccinium* c. 40 cm high, on shallow peaty skeletal soils, 6 July 1988, H. Noltie (E); same locality, 18 July 1988, A.C. Jermy No. 18075 (BM, NMW). Subsp. *alpinum* not associated but within 100 m, on more open alpine heath.

V.-c. 96 Easternness: S.W. slopes of Geal Charn, Glen Feshie, 2700 ft [810m], on open heather moorland on granitic soils, J.A. Wheldon and A. Wilson, July 1909 (BM, BRIST, CGE, E, OXF, NMW). Searched for many time since unsuccessfully, but could still be there.

V.-c. 100 Arran: Glen Easan Biorach, at about 1000 ft [300m] altitude, A. Somerville, 2 July 1895 (E, OXF). Not collected since.

Lochransa, Terras herb., 1884 (E). Most likely the same locality as above. Not seen since, but this or these could well be there still.

V.-c. 104 North Ebudes: Skye, "Cuillins", M.A. Lawson, July 1868 (BM, CGE, OXF). Nothing approaching this taxon has since been collected on Skye but obviously there is great potential for it to be there.

V.-c. 108 West Sutherland: Canisp, on lower slopes at c. 270m alt., amongst boulders in dwarf heath vegetation, July 1985, A.G. Kenneth (BM, E); July 1987, D.J. Tennant & A.G. Kenneth (BM). On a mountain with much *alpinum*, the *issleri* population was distinct in the colour and rigidity of the vegetative branches and showed sporing branches with long-pedunculate cones, often branching at their bases (see Fig. 2). An extensive survey made of the site, and both around and above it, by Archie Kenneth and David Tennant

(pers. comm.) in 1987, revealed variation in the *alpinum* populations, which suggests possible interbreeding. The area has much potential for further research and may well hold *complanatum* itself.

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I am grateful to the late Archie Kenneth whose friendship I had enjoyed for many years and who re-kindled my interest in this problem through finding such an excellent site in Sutherland, the discovery of which was a further example of his astute field observation. I am also indebted to David Tennant who has kindly read this manuscript, and whose acute observations on the Canisp plants were freely given to me and have been incorporated into this paper. I am also grateful to Dick Roberts for allowing me to quote his spore measurements, and to Noel King for his notes on the Worcestershire plant and site.

I would like to thank the Director of the Botanisches Institut der Universität Basel, and Drs Christian J. Heitz and Tadeus Reichstein, for providing photographs of Issler's specimens held in the Basler Botanische Gesellschaft herbarium. The Editors of the *Gazette* made constructive comments on this paper for which I am grateful.

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REVIEW

PTERIDOPHYTE FLORA OF OAXACA, MEXICO by John T. Mickel and Joseph M. Beitel. 568 pp. *Memoirs of the New York Botanical Garden* volume 46. 1988. ISBN 0 89327 323 6. Price \$94.85 for U.S. Orders, \$96.80 for non U.S. Orders.

The Introduction to this book outlines the development of fern floristics for Mexico over the past 150 years. From 182 species reported by Martens and Galeotti in 1842, we learn that there are now 690 species known in Oaxaca alone out of a present estimate of 1000 or more for the whole country.

The complex physiography of this State has much to do with patchy fern collecting in the past, as well as the wide natural taxonomic diversity of the fern flora recently revealed. Moreover, the range of ecology and the discrepancies in the known flora between this and neighbouring States, suggest that primary exploration still has much to yield.

Oaxaca is phytogeographically at a crossroads between the Caribbean elements of the wet windward slopes of the mountain ridges, the arid 'cheilanthoid' flora stretching from the north and Central Mexico, and the tropical Central and South American components extending to their northernmost limits.

The largest genera, *Asplenium* (55 spp.), *Thelypteris* (45 spp.), *Cheilanthes* (44 spp.), *Selaginella* (39 spp.), *Polypodium* (37 spp.) and *Elaphoglossum* (33 spp.), (nearly 37% of the flora in 6 of the 101 genera in 27 families represented) demonstrate clearly, in whole or in their parts, the varied ecological characteristics of this fascinating region.

Descriptions of species are mostly concise and adequate, being sometimes shortened and diagnostic for rare or closely related taxa. Explanatory notes are frequent especially for new names of which there are about seventy including new species (described here for the first time), hybrids, some varieties and, happily, no subspecies. Groups of closely related species often have a note following one member of the group entailing cross-reference and much turning of pages because of the alphabetical sequence. The book has alphabetical arrangement of genera and species throughout. This leads to a comment on the choice, quite clearly made by the authors, to 'ignore families' because 'utility should be the prevailing guide in selecting an arrangement'.

But what is utility? An alphabetical catalogue is useful for someone who wants to establish quickly a fact or two about a plant of which the name is already known.

Illustrations, especially first-class fully vouchered line-drawings, like the 129 plates at the end of this book, are useful imperatives in providing visual affirmations of appearances and relationships. Here, they are arranged according to a cryptic conspectus of 27 families at the beginning of the book. What happens in between has nothing to do with this or any other system.

Utility is in no way better served than in systems of classification. They have the purpose of summarizing the characters of groups within groups as a shorthand to learning and research in intellectual processes. The foundation of their intrinsic merit, a normal expectation in a Flora, is totally lost in the cheerless formality of the alphabet.

Regrettably, there are precedents for this, and even more regrettably they come from the professional eminence of the Flora-writing fraternity. There is, as our authors state, 'widespread disagreement among pteridologists regarding familial and generic phylogenetic arrangements (of ferns).' But has this book been prepared so diligently and painstakingly for pteridologists only? How many aspiring pteridologists are there in the State of Oaxaca? Are the shorthands and mnemonics of botanical systematics irrelevant to students and other interested people, even other botanists, in Mexico and elsewhere? Of the 27 families in the 'cryptic conspectus', 17 are quite indisputable in their circumscription. The other 10

COMPRESSION AND SLINGSHOT MEGASPORE EJECTION IN *SELAGINELLA SELAGINOIDES* - A NEW PHENOMENON IN PTERIDOPHYTES

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ABSTRACT

Observation of the megaspore and microspore dispersal mechanism of *Selaginella selaginoides* shows that the release of the two types of spores takes place by very different methods.

Microspore discharge takes place passively, while megaspore dispersal takes place by an active discharge mechanism, termed here 'compression and slingshot ejection'.

No active megaspore ejection has, as far as I am aware, been hitherto reported in this or any other heterosporous pteridophyte genus.

This mechanism is discussed and interpreted in relation to the outlying taxonomy, ecology and palaeobotanic history of *Selaginella* and is suggested to be a primitive and perhaps ancient evolutionary trait within the genus.

INTRODUCTION

Selaginella selaginoides (L.) Link is a small, moss-like plant, which occurs widely amongst low-growing vegetation throughout a circum-boreal range (Polunin 1959, Page 1988). It is also one of the very few pteridophytes in the native flora of Britain and Ireland which is heterosporous. Each cone, which matures in Scotland by mid- to late August or early September, usually bears an assortment of microsporangia and megasporangia in the axils of its weakly-differentiated, leaf-like sporophylls. Sometimes sporangia of each type occur somewhat randomly within a cone. More often, microsporangia and megasporangia are zoned within each cone, with the megasporangia always at the base, and sometimes there are multiple zones of micro- and megasporangia, especially in larger cones. At maturity, the simple, globose microsporangia each liberate a large number of small, orange microspores; the 4-lobed megasporangia each liberate only four large, white megaspores. Microspore discharge takes place passively, while megaspore dispersal takes place by an active discharge mechanism, termed here 'compression and slingshot ejection'.

Although an active microspore-dispersal mechanism has recently been reported in some tropical *Selaginella* species (Koller & Scheckler 1986), no active ejection of megaspores has, as far as I am aware, been hitherto reported in this or any other heterosporous pteridophyte genus.

This mechanism is discussed and interpreted in relation to the outlying ecologic, taxonomic and palaeobotanic position of *S. selaginoides*, and is suggested to be a primitive and perhaps ancient evolutionary trait within the genus.

MATERIALS AND METHODS

The phenomenon of sudden, ballistic, megaspore ejection in *S. selaginoides* was initially discovered by the author by simple hand-lens observation of *in situ* specimens in the field in East Perthshire, Scotland. Subsequent further *in situ* observations made on more than 50 wild, mature specimens showed it, indeed, to be a general phenomenon of the species throughout its range in Highland Scotland.

Supplementary laboratory observations were made on isolated cone material transferred when freshly gathered in August 1987 and August 1988 to laboratory environments at Kindrogan Field Studies Centre, Perthshire and to the Royal Botanic Garden, Edinburgh, Scotland, respectively, enabling the exact sequence of events to be more precisely studied. Megaspore discharge distances quoted were those achieved in a laboratory atmosphere, measuring from the position of the cone to the final settlement point of the megaspore from a still atmosphere on a smooth dark surface.

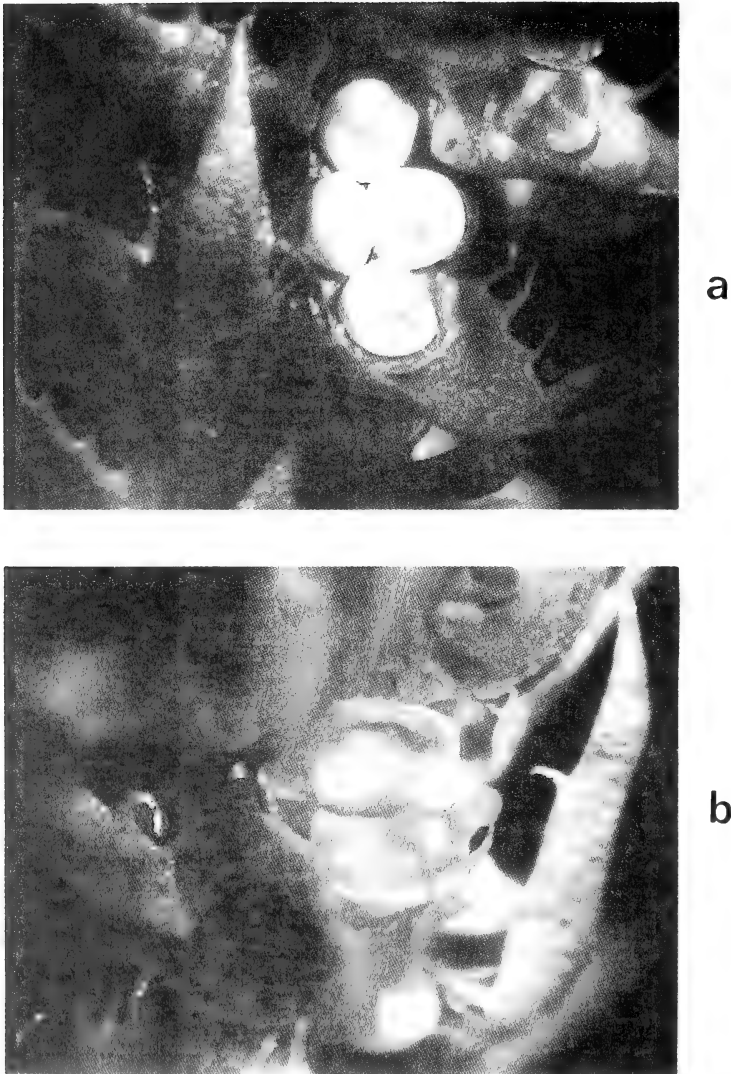


Fig 1, a - b 'going, going, gone!'; a: Megasporangium walls fully withdrawn from around a quartet of megaspores, to the point of being fully primed, with the megaspores on the point of sudden and violent release; b: the moment immediately following discharge, with the now-empty megaspore cradles formed from the original megasporangium wall showing the large upper and lower lobes and the much smaller lateral ones (x 64). Photos: C.N. Page.

OBSERVATIONS

Compression and slingshot megaspore ejection

Each microspore of *S. selaginoides* is c. 30 μm diameter, each megaspore c. 690 μm diameter, the megaspores being thus approximately 23 times the diameter of the microspores, and over 12,000 times their volume. Indeed each megaspore is thus sufficiently large to be clearly seen with the naked eye. SEM details are well illustrated by Tryon (1949: 424).

Field and laboratory observations on native Scottish material show that although the

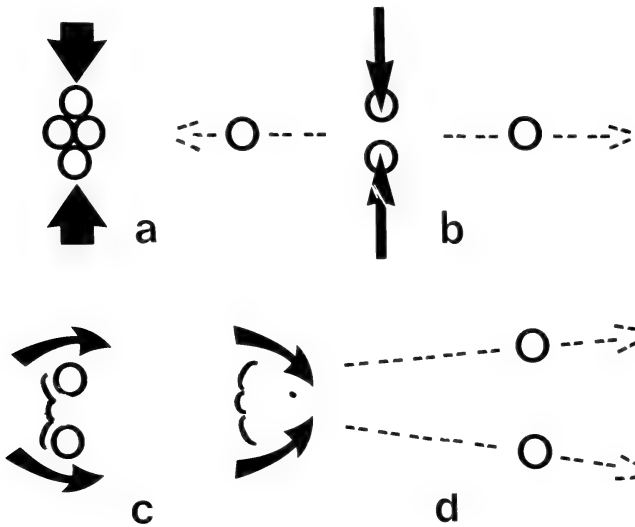


Fig 2, a - d, diagrammatic representation of the megaspore discharge sequence of *Selaginella selaginoides* described here; a - b, FRONTAL VIEW, a: quartet of megaspores with central pair becoming squeezed by compression action between the upper and lower megaspores in the axil of a deflexed megasporophyll (thick solid arrows indicate main compression force directions); b: central megaspore pair suddenly ejected as a result of this compression action; c - d, SIDE VIEW, c: larger arms of megaspore cradle carrying the upper and lower megaspores snap forward as an immediate result of loss of the central megaspore pair; d: the upper and lower megaspores are hurled violently from the cone by the slingshot action resulting (slender solid arrows indicate direction of initial megaspore and cradle movement, thin dotted arrows, the ultimate direction of megaspore ejection).

microspores are dispersed at maturity in a totally passive fashion, megaspore dispersal takes place by an active discharge mechanism, termed here 'compression and slingshot ejection'. By this mechanism, the megaspores of each ripe megasporangium are shot ballistically from the plant, dispersing them to greater distance than would be likely to be achieved by passive dispersal alone, as well as through a wide radial settlement pattern.

This discharge process is always similar and spectacular. It is best analysed in three phases: that of megasporophyll priming, that of megaspore ejection, and that of the dispersal distance achieved by the resulting megaspore trajectories.

Megasporophyll priming

The megaspore discharge process of *S. selaginoides* involves the once-only (for each megasporangium) sudden and virtually explosive release of what appears to be the slowly accumulated tension acquired by successive megasporophylls.

Each megasporangium, with its adjacent megasporophyll, acts as an independent discharge system. Tensioning of the system appears to be initiated by the shrinking and eventual splitting of the ripe megasporangium walls. As these shrink, so the whole megasporangium becomes drawn progressively deeper into the axil of its subtending megasporophyll blade, forcing the four megaspores contained within tightly together. This axial retreat of each mature megasporangium causes a gradual backward-flexing of the whole subtending megasporophyll blade, which consequently becomes forced into an increasingly divergent angle from the axis of the cone. As it becomes deflexed, it appears to become increasingly tensioned. Indeed, even casual observation of almost any fully mature cone of this species

in the field typically shows one or more deflexed megasporophyll blades standing at an abruptly divergent angle from those of the rest of the cone, although no significance has, as far as I am aware, ever been previously attributed to this. Only megasporophyll blades appear to do this, and each only once, when the megasporangium in their axil is fully mature and about to dehisce. It appears to be this gradually accumulated tension which ultimately powers the whole ejection event.

The duration of the period of tensioning varies according to the speed of splitting and shrinkage of the mature megasporangium wall, and hence with the humidity of the air. In a dry laboratory atmosphere, it usually took place fully over the course of about a 2-minute period. In the field, periods of from 5-30 minutes or more seem more usual.

As the tensioning of the megasporophyll blade proceeds, so the shrinking megasporangium wall, splitting along approximately X-shaped predetermined lines of weakness, separates around the spores into four discrete arms. Each resulting arm clasps, but gradually withdraws from, around one megaspore, by slowly sliding back to form a cradle around its megaspore's periphery. At this stage, the megaspores can be seen to be arranged as two decussate pairs: a medial pair, lying in the plane of the midvein and cone axis, and a lateral pair, lying perpendicularly to the first pair and withdrawn partly between them (Fig. 1a).

Drawn maximally into the angle between the cone axis and the deflexed megasporophyll blade, the quartet of megaspores in the fully-tensioned system appears to be subject to especially strong compressive forces between the tightening megaspore cradle arms, which themselves are compressed within the axil of the megasporophyll blade. The lateral pair of megaspores are especially tightly compressed between the two medial megaspores which squeeze their sides, and the tips of their megasporangium walls, which still just retain them. The megaspores themselves are hard and rigid objects, and appear not to easily distort to this compression. Under a low power microscope, isolated megaspores can be seen to have walls which are externally ornamented only by low, rounded, projections. But when newly revealed by the withdrawing megasporangium wall, the fresh spores in life have a smoothly glossy appearance and apparently moist surface. Indeed, as the megaspores become progressively more visible, they look like a clutch of four, shining, wet eggs, held in a tight and shrinking nest.

Once fully primed, with the megasporophyll blade deflexed to an angle of about 80° from the cone axis, and each megaspore largely revealed, but still held around its periphery by the embrace of one arm of the retreating megasporangium wall, the whole system is ready to actively eject the megaspore quartet revealed (Fig 1a).

Megaspore ejection

Sudden total release of the slowly accumulated tension occurs when the four mature megaspores are shot forcefully from the plant, in two rapidly-successive (ie split-second) volleys.

Compression ejection of the first megaspore volley: Discharge of the first megaspore volley is initiated when the steadily retreating margins of the splitting megasporangium wall eventually lose their last vestiges of grip on one opposite (always lateral) pair of megaspores; for the arms of the megaspore cradle retaining this lateral megaspore pair are always much smaller than those retaining the central pair (see below), they are thus always the first to finally lose their grip. At this critical point, the now tightly compressed, round and apparently moist-surfaced, lateral megaspores are suddenly and forcefully ejected as a pair from the megasporangium, in a manner analogous to two round bars of wet soap being equally suddenly and forcefully ejected from a pair of squeezing hands!

Slingshot ejection of the second megaspore volley: With the sudden loss of the first megaspore pair, which had, during priming, been forcing between them, the remaining medial pair of megaspores are hurled from the cone by each of their spoon-shaped wall portions snapping sharply forward with a rapid slingshot-action, now fully releasing the remaining tension between the cone axis and the formerly deflexed megasporophyll blade. Discharge of the second megaspore volley is initiated immediately by the loss of the first spore pair, and thus always follows in nearly-instant succession; their larger pair of cruciate arms of the original wall (see below), forming spoon-shaped, sling-like cradles now snap sharply together, hurling the two remaining megaspores from the cone as they close. The sudden ejection of this second megaspore pair is thus like projecting two wet plums from two facing tablespoons, each held at its handle-base and tensioned by pulling back the spoon-tip! (Fig. 2 c-d).

Once all the megaspores have been ejected, the relative sizes of the two pairs of cruciate arms of the original megasporangium wall can now be most clearly seen. The lateral pair are always the smaller, and the medial pair always the larger and more spoon-shaped. (Fig. 1b). The former function to retain their megaspore pair only until overcome by increasing compressive forces, the latter act as cradles to then eject their megaspore pair by their different slingshot action.

Dispersal trajectories

The resulting discharge distances of the trajectories achieved for the size of the plant are impressive. In a still, dry, laboratory atmosphere, trapping of ejected spores on sticky plates, held inverted above erect cones, indicates that megaspore ejection can take place to a vertical height of 1 metre or more, and that such ejected megaspores, when allowed to land from their trajectories, arrive with a random distribution radially around the parent cone at distances of mostly 5-45 cm, with a few reaching over 65 cm distance.

Air-resistance against a moving body of such low mass must be a potent factor in slowing its velocity rapidly. However, the laboratory distances measured are those achieved in still air, and take no account of the field-situation in which the whole cones and ejected megaspores of *S. selaginoides*, as well as its passively-released small microspores, in bleak upland wild habitats, are more or less constantly subjected to considerable crosswind forces. It may, indeed, be such passing breezes which, under field conditions, are effective in promoting the initial desiccation process leading to the megaspore discharge event. Further, such breezes not only serve to disperse the passively-released microspores, but also quite actively agitate the direction of orientation of the cone itself, thereby probably greatly increasing the total radial component of the trajectory of megaspores which become ejected at varying radial angles into the passing (and probably turbulent) moving air.

To imitate wind-oscillation, when cones of *S. selaginoides* were experimentally held in the laboratory at varying angles to the vertical, horizontal megaspore discharge distances were found to be greatly increased, and horizontal settlement distances of from 1.5 to over 2 metres from the cone were regularly achieved, with a few megaspores occasionally being shot to horizontal distances of over 3m from the parent cone!

Cone-agitation by crosswind forces thus probably plays a significant role in increasing both the absolute distance and randomness of radial direction in which the megaspores are finally hurled.

DISCUSSION

Although this 'compression and slingshot' method of spore ejection is a structurally simple one, it is impressively effective in hurling the large megaspores of this small-statured species over appreciable airborne distances, and through a wide radial range of scatter pattern. The actual speed of ejection of the spores from the plant (the equivalent of the "muzzle

velocity" of a gun) must be considerable, considering the small megaspore mass and the height and distance to which each megaspore is shot. Indeed, impingement of the suddenly-ejected spores as two successive volleys can certainly be felt on the face of the close observer. It also seems to have aspects of considerable biological and palaeobotanic significance.

Ballistic aspects

Various mathematical formulae have been proposed to describe the distribution patterns of both passively dispersed spores and the ballistics of spores which are violently ejected, the latter especially resulting from observation of fungal mechanisms (see, for example, Buller 1909, Gregory 1945, 1951, 1961, Ingold 1965, 1971, Gregory & Stedman 1953, Schrodter 1960 and Sreeramulu & Ramalingen 1961).

From the aggregate of such studies, two general principles applicable to the contrasting spore types of *Selaginella* seem to emerge:

One is that for passively dispersed airborne spores, relatively random downwind dispersal patterns may be anticipated, analogous to a smoke plume, beneath which is likely to be an approximately logarithmic decrease in settlement density linearly away from the spore source in a unidirectional, narrowly triangular downwind pattern. Absolute dispersal distance for any spore is likely to be strongly influenced by a multiplicity of environmental variables. For achievement of highest dispersal distance, smallness of size promoting slow settlement rates and hence long airborne times, is likely to be of high selective advantage, and, indeed, the microspores of *Selaginella* would appear to fall well within an effective operational size for such anticipated missions.

By contrast, the second principle to emerge seems to be that the subsequent trajectories and settlement patterns of violently-ejected spores are somewhat more mathematically predictable (if more complex to calculate), with a generally circular pattern of expected settlement patterns (modified to perhaps a more ovate shape by crosswinds) reaching a maximum density away from the source at a predictable radial distance. Also by contrast with microspore size, for highest dispersal distance and for minimum influence to trajectories of the vicissitudes of wind currents and air turbulence, rapid speed of ejection as well as relatively large mass would be at a strong selective advantage. The size of the megaspores of *S. selaginoides* certainly appear to be within an adequately massive operational size for their very different dispersal mechanism to operate effectively in the field.

Ecological and biological aspects

In Scotland, the erect cone-shoots of *S. selaginoides* normally arise to about 1-4 cm above the level of the ground. Its montane habitats, as well as its coastal dune ones, are sites which are not, and probably have never been, covered by extensive tree growth in post-glacial time. Further, it is very probable that *S. selaginoides* was once a widespread species of early post-glacial habitats, characterised by their open vegetation, before the extensive development of tree vegetation in Britain and Ireland (Page 1982, 1988), and, indeed, exposure of habitats, appears typical of the plant throughout much of its modern, boreal range. Were its megaspores merely passively released, at heights of under 4 cm above ground level (and often among other low-growing herbage), their opportunity for more effective dispersal by wind currents might well be appreciably limited. Ejected into the air, however, not only is more distant dispersal likely to be regularly achieved, but so also is a far better radial directional scatter of megaspores through wind-agitation of the cone.

Biologically, the significance of this process is presumably not only in removing the sites of new megaprothallial establishment (and hence the site of origin of new sporophytic progeny) well away from the parent plant, but also in increasing the opportunity for randomness of fertilisation of the resulting megaprothalli by the antherozoids of independent microprothalli deriving from passively-dispersed microspores originating from independent, differently-placed, upwind, sporophytes. For only when so-removed, in large part, from

settlement within the same downwind dispersal zone as that of a sporophyte's own microspores, do the biological benefits of heterospory in an airborne environment seem likely to become most fully realised.

Elsewhere in the genus, in a wide range of tropical species of *Selaginella* examined by Koller & Scheckler (1986), no active megaspore ejection mechanism was detected, nor, so far as I am aware, has nay been by any other author on *Selaginella*, and it seems possible that this may indicate a real absence of this phenomenon amongst the tropical species. In these species, a more active microspore dispersal system, however, exists, and as such it would seem that in these taxonomically very different groups of *Selaginella* (the species-poor homophyllous one and the species-rich heterophyllous one), a similar biological result has probably been achieved by specialisation within each group in violent dispersal of one (opposite) spore type only. For it perhaps matters less, biologically speaking, how the two types of spores are actually discharged, so long as they are removed from the site of the parent plant and that they are discharged in ways that achieve significantly different settlement patterns.

Taxonomic and palaeobotanic aspects

Within the genus, *S. selaginoides* is taxonomically a highly distinctive member, with cylindrical cones, homomorphic leaves and spiral phyllotaxy, there being only one other living species (*S. deflexa* Brack. of the Hawaiian Islands) with a similar general morphology. The sporangial arrangement, with a basal megasporangiate zone and a superior microsporangiate one, is also restricted within the genus to this pair of species (Horner & Arnott 1963). These aspects and the relatively undifferential foliar trait of *S. selaginoides* (which also includes very leaf-like sporophylls) has been taken to indicate primitiveness within the genus as a whole (eg Bower 1908, 1935: 288, Smith 1938, Thomas 1985, Jermy in press). It thus seems possible that this 'compression and slingshot' megaspore ejection mechanism may itself be ancient within the genus and as such could have existed in similar form in early members of *Selaginella*.

At the family level, Selaginellaceae (the only family of the Selaginellales – Thomas & Brack-Hanes 1984) appears to have been separate from Lycopodiaceae since at least the Lower Carboniferous. For, by this time, heterospory amongst ligulate clubmosses with radial shoot symmetry had already evolved (Bower 1908, 1935, Hirmer 1927, Smith 1938, Boureau 1967, Stewart 1983, Thomas & Spicer 1987), while there is also evidence of perhaps even more primitive ligulate lycopods from as early as the middle Devonian (Grierson & Bonamo 1979).

At the genus level and below, heterophyllous and homophyllous groups of *Selaginella* appear to have been separate since at least the Upper Carboniferous (Thomas 1985 & pers. comm. 1989), from when, as with the other probably equally ancient pteridophyte genus *Equisetum* (Equisetaceae) (Page 1972), small herbaceous forms of *Selaginella* may well have survived relatively unchanged to the present day (eg Taylor 1981, Thomas 1985). Evidence for the early existence of small, *S. selaginoides*-like forms comes from several independent sources. Bower (1908), for example, first drew attention to the work of Benson (1907), who compared a small Carboniferous plant of lycopod-like form, *Miadesmia membranacea*, with the habit of living *S. selaginoides*, although the megasporangial characters appear to have been even more advanced (see below). Another Carboniferous fossil, *Selaginella fraipontii* was also clearly a plant of herbaceous form and probably sprawling habit (Schlanker & Leisman 1969), while comparisons have also been made of the Carboniferous *Selaginellites crassincinctus* (Leisman 1961) and of *Paurodendron* (Phillips & Leisman 1966) with the living *S. selaginoides*, underlining further the morphologically primitive status and probable very great antiquity of the herbaceous habit and general homomorphic form of living *S. selaginoides*.

Through the fossil record, with the evolution of heterospory, the number of megaspores

per megasporangium has been different in different taxa. Even today, some *Selaginella* still show occasional variation in megasporangial number (eg Duerden 1929), while the fossil record shows many possible past avenues of evolutionary opportunity in terms of megaspore-reduction numbers. Some of the Carboniferous taxa of *Lycopodites* (subsequently put into *Selaginellites*) reported by Bower (1908: 301) had 16 or 24 megaspores per megasporangium. However, by as early as the Carboniferous, the present-day number of *S. selaginoides* had already been achieved in *Selaginella fraipontii* (Schlanker & Leisman 1969), while this number was modified still further in the arborescent Lycopod *Lepidophloios*, by reduction of the developing tetrads to one and the subsequent abortion of three of its members, although in this case, the resulting single mature megaspore is believed to have been discharged complete with its sporophyll as an airborne unit (Thomas 1978, Thomas & Spicer 1987). The megaspore number was also reduced to one in the herbaceous *Miadesmia membranacea* (Benson 1907, Bower 1908) – see below.

The data from living *S. selaginoides* suggests that, for the microspores of this species, and presumably for those of the fossil forms, evolutionary selection pressure has probably always favoured smallness in size and low mass to maximise airborne dispersal opportunity. But for airborne megaspores, once larger than a critical size above which passive wind dispersal is less effective, selection pressure would seem likely to have favoured the evolution of more massive projectiles, and that of an efficient ejection mechanism, helping ensure different spore settlement patterns and thereby maximising opportunity for outbreeding between prothalli from different original sporophytes.

Evidence from the fossil record certainly provides abundant indications of widespread trends to reduce the megaspore number per megasporangium, while increasing its size and mass. It would be of interest to know whether any cone specimen in the long history of these fossil heterosporous clubmosses also showed evidence in the form of occasionally deflexed megasporophyll blades, or of discharged megasporangial walls of regular structure, indicative of the past presence of active megaspore ejection systems.

Finally, the strategic advantage of mass in a ballistically-ejected megaspore projectile would also open opportunity, should it be of subsequent selective advantage, for increase in biological reserves. In this connection, it seems of interest to note that Bower (1908: 300), although he did not know of the megaspore ejection mechanism described here, compared the Carboniferous *Miadesmia membranacea* with living *S. selaginoides*, but pointed out the principal difference that *Miadesmia* bore in its megasporangia not four megaspores, but what is described by Bower as 'a single, seed-like structure' (on the basis of Benson's observation that it germinated *in situ*, presumably into a megaprothallus) (Benson 1907). Once an efficient megaspore ejection mechanism had evolved, it would not be too big a step to conjecture such a mechanism then advantaging the further evolutionary step that *Miadesmia* suggests, of reduction to a single megaspore, retained through germination to a simple prothallus within the protection of its megasporangium, pollinated *in situ* by the germination of airborne microspores, and the whole fertilised-product then efficiently ejected as a simple seed.

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Contd. from p. 266

are a backlash against the artificially unitary, and actually polyphyletic 'Polypodiaceae' of more contented days. Here lies the main cause of the disagreement, but the 'Polypodiaceae' did no injustice to the uninitiated, and so it must be the professionals who are floundering in their own confusion. This should not be a position to retreat from but rather another opportunity to test an existing system, or to try yet another new one. There is much more information available to-day than there ever was in the past, and there are much easier ways of sorting it.

The indefinite prospect of putting up with Catalogues rather than Floras, while we wait for a perfect system agreeable to all, is an undesirable alternative.

The contents of the book are most comprehensive and are the result of years of meticulous research. It is a beautifully produced volume of which the authors and publishers should be deservedly proud.

C. D. ADAMS

SHORT NOTE

DRYOPTERIS × *FRASER-JENKINSII* – A CORRECTION

The name *Dryopteris* × *fraser-jenkinsii* was invalidly published in a recent article (Gibby & Widén 1983) because a holotype was not properly indicated, and this is now corrected:

Dryopteris × *fraser-jenkinsii* Gibby & Widén, *hybrida nova*

Holotypus: ex hort. Chelsea Physic Garden, CPG 2189, 25 August 1981 (BM), originally from Spain, Oviedo, beside road from Aviles to Ribadeo, by bend in road, 1km S. of Canero, E. of Luarca, 50m alt., mixed *Pinus*, *Quercus* and *Castanea* forest, with *D. affinis* (Lowe) Fraser-Jenkins, *D. dilatata* (Hoffm.) A. Gray and *D. guanchica* Gibby & Jermy, coll. C.R. Fraser-Jenkins 4899, 5 June 1976.

Isotypus: (M).

Hybrida in morphologia *D. affinis* similis. Pinnulae autem plus dissectae ad costam fissae, segmentis rotundatis dentatisque. Sporae pleraeque abortivae, vix 5% ut videtur bene evolutae et haec grandes, rugosae eis *D. affinis* similes sed nonnumquam subspineae vel spinulosae.

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AN ABERRANT FORM OF *EQUISETUM TELMATEIA* (PTERIDOPHYTA) FROM THE WEST OF IRELAND

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ABSTRACT

A population of *Equisetum telmateia* in Co. Clare, Ireland, was discovered to have a number of shoots which produced a proliferation of small cones. These specimens were examined and found to have apparently viable spores. Speculation is made that this type of cone production may provide a link to extinct horsetails.

INTRODUCTION

During a visit to The Burren, Co Clare, a population of *Equisetum telmateia* Ehrh was found at Clifden Hill (National Grid of Ireland 127189) on 6 June 1988. Several unusual fertile shoots were present which bore whorls of small cones. The phenomenon of proliferating cones is rare, but has been recorded by Pope (1983) in a population of *E. telmateia* from the Isle of Wight, and in various forms and species by Page (1972).

SITE

The aberrant specimens were part of a vigorous population of *Equisetum telmateia* growing along ditches on both sides of a minor road. The *E. telmateia* was the dominant species between the ditches and the hedges behind for a distance of about 1 km. The road was about 100 m above Ordnance Datum and was situated on a slope between the acidic recently glaciated shale lands and the Carboniferous Limestone of the Burren (Willmot 1979). Associated species included the calcicol indicators *Polystichum setiferum* and *Asplenium (Phyllitis) scolopendrium*. *Equisetum palustre* was also present.

SPECIMEN DESCRIPTION

Morphology

The aberrant fertile shoots possessed nodal branches and had a mean height of 90cm, which was generally 10-20cm smaller than wholly vegetative shoots. Fertile stems had senescing apical cones which were similar in appearance to normal *E. telmateia* cones, and the upper branches carried small cones in whorls around the nodes (Fig. 1). The proliferating cones varied from being well filled and terminating short branches (Fig. 2a), to shrunken vestigial cones which had reverted to branches (Fig. 2b), or intermediates between these conditions. Some lower branches carried two successive cones, (Fig. 2c). Frequently the vegetative branches bore further lateral branches (Fig. 1). It should be noted that some branch-bearing stems were found which bore single, fertile apical cones, but lacked any proliferation of cones around the nodes.

Spores

Under a light microscope, sporangia of the smallest cones generally appeared fused and shrunken, particularly in cones which had reverted to branches. Sporangia from apical and larger, non-apical cones produced some abortive material, but many good spores with elaters, chlorophyll and a spherical shape were also present (Fig. 3). The ratio of apparently viable spores to abortive material tended to increase with cone size, but variation was also found between sporangia within a single cone.

DISCUSSION

The Burren population differs from that found in the Isle of Wight in that Pope (1983) reported small cones only on the tips of proliferating side shoots, while Burren specimens

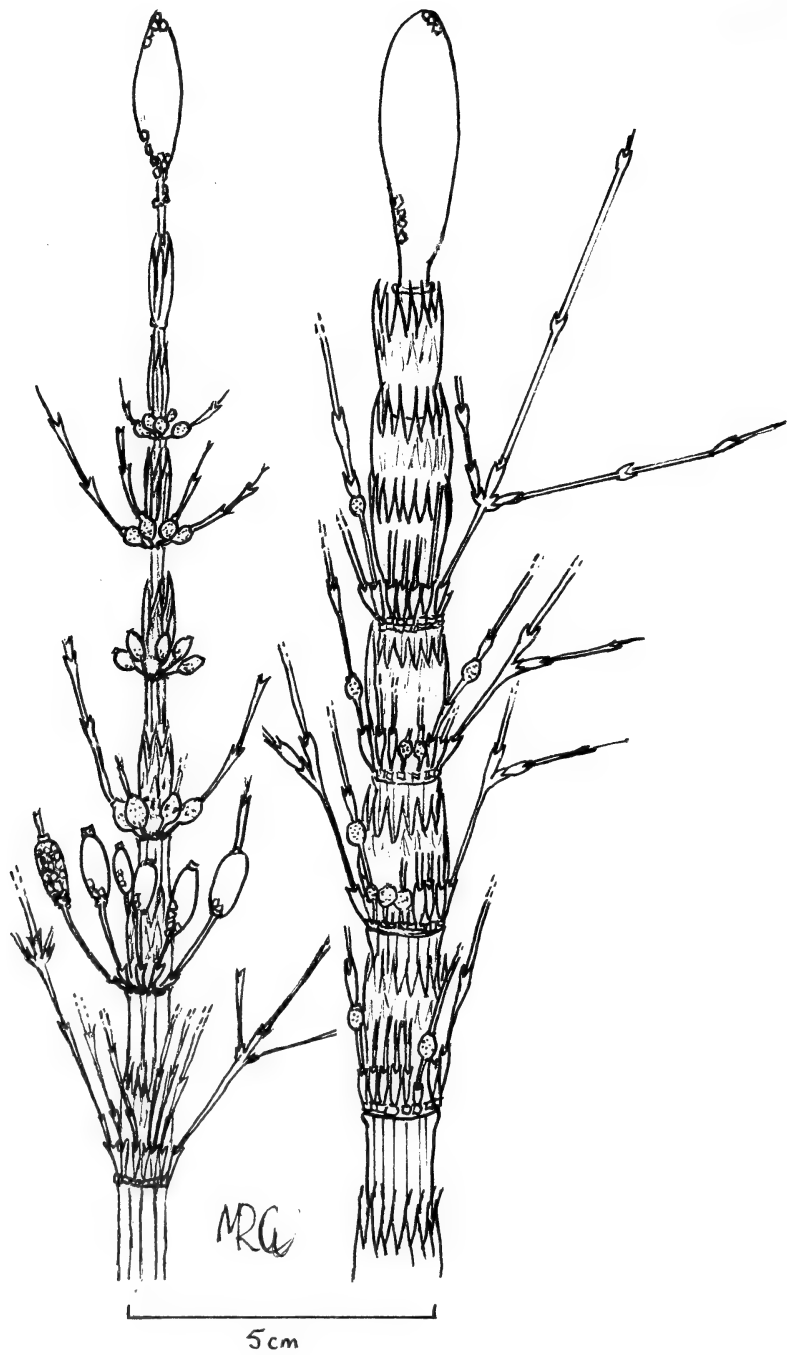
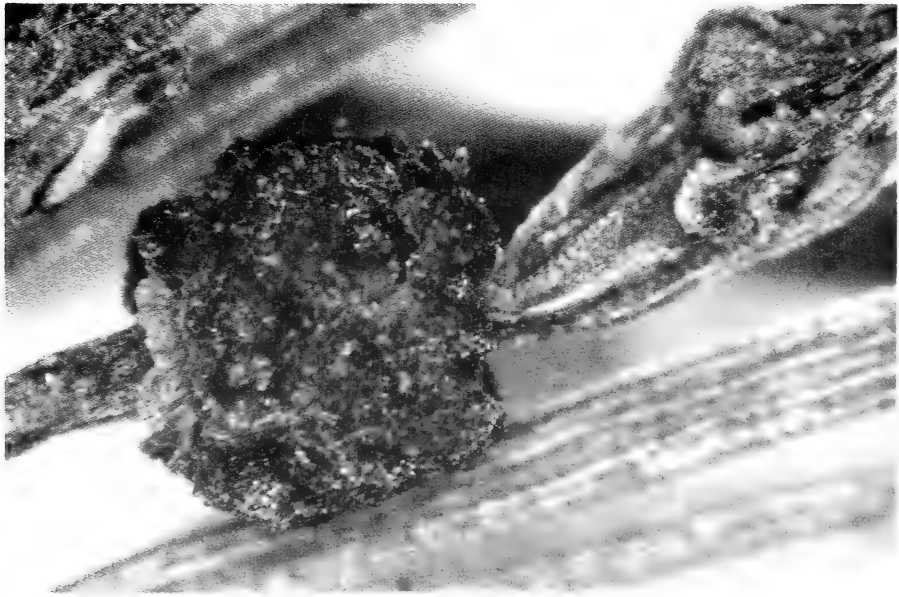


FIGURE 1. Overall structure of aberrant fertile shoots of *Equisetum telmateia*, Clifden Hill, Co. Clare. Note the many small intercalary cones.



a



b

FIGURE 2. Details of cone proliferation in *Equisetum telmateia*.

(a) cones from upper nodes with well filled sporangia (x 32).

(b) vestigial cone reverting to branch (x 160).

(c) alternation between vegetative and fertile growth on the stem node branches (x 32).



C FIGURE 2(c).



FIGURE 3. Spores from a larger proliferating cone of *Equisetum telmateia*, showing apparently good morphology (x 2500).

alternate from cone, to branch, to cone. Mr B. Robson (personal communication), has reported that the production of multiple cones occurs annually on the site, therefore the specimens are not the result of a single isolated abnormality.

Page (1972) and Page & Baker (1985) note that *Equisetum* species have a high degree of morphological plasticity, which this find reflects. The proliferation of cones reverting to shoots is reminiscent of some horsetails known from the fossil record, eg the Permian *Phyllothea deliquescens* (Goeppert) Schmalhansen (Boureau 1964: 398), the Upper Permian *Equisetinostachys grandis* Rasskazovo (Boureau 1964: 414) and the Upper Triassic *Equisetites* (*Equisetostachys*) *bracteosus* Kon'no (Kon'no 1962; Boureau 1964: 435). Populations of this type may indicate that the divergence of extinct and modern horsetails may be less than often believed.

ACKNOWLEDGEMENTS

I am grateful to Dr C.N. Page and Dr J. Proctor for their help.

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REVIEW

AZOLLA UTILIZATION (Proceedings of the Workshop on *Azolla* use, Fuzhou, Fujian, China, 31 March-5 April 1985). Edited by W.H. Smith and Emerita Cervantes. International Rice Research Institute, Manila 1987.

The cultivation of *Azolla* with rice is traditional in China. It provides supplementary nitrogen to the rice crop, suppresses weeds by shading, and provides food for fish and ducks. It can be harvested and fed to pigs and domestic fowls. This is the report of an international symposium on the cultivation and use of *Azolla*. In India this practice is increasing; dried cow dung and powdered neem cake are used to encourage growth of the fern, which has a high phosphorus requirement. Programmes to encourage the use of *Azolla* are in being in the Philippines, elsewhere in Asia, and in Africa and in South America. There are problems to be overcome; the plant does not thrive at high temperatures, and it is subject to a number of serious insect pests. In Japan *Eichornia* is preferred as a rice nitrogen source and as animal feed. This report is a useful summary of the present state of knowledge in this subject.

F.H. BRIGHTMAN

A NEW SPECIES OF *SELAGINELLA* (PTERIDOPHYTA) FROM CAMEROON, WEST AFRICA

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ABSTRACT

Selaginella serrato-squarrosa Quansah, a new species from Cameroon, is described and illustrated.

INTRODUCTION

In his account of the genus *Selaginella* Beauv. in West Africa, Alston (1959) listed 20 species. A recent taxonomic revision of the genus in West Africa and Madagascar by the author, Quansah (1986), has revealed one new species from Cameroon:.

Selaginella serrato-squarrosa Quansah, sp. nov. Figure 1 & 2

Species *Selaginella heterophylla Selaginellae squarrosae* Baker similis sed ab illea foliis marginibus serratis, foliis mediis aristatis longe (arista laminae duplo longiore, strobilis aut omnino microsporangiatis aut sporophyllis dorsalibus megasporangiatis microsporangiatisque et sporophyllis ventralibus omnino microsporangiatis.

Typus: CAMEROON, Edea, c. 1500m on moist forest floor, 28 April 1948, Nicklès 102 (P, holotypus).

Plants erect/sub-erect; branch-system 3-5 pseudopinnate; rhizophores arising at the axils of primary branches and restricted to the basal two-thirds of the plant. Leaves anisophyllous, single-veined; ligules up to 0.45 mm long, elongate pedate, occasionally bifid. Lateral leaves asymmetrical, sub-subulate to ovate-oblong, up to 5.3 x 1.6mm base sub-attenuate to oblique, apex acute, margins of basal third serrate-entire, apical two-thirds entire/sub-entire; amphistomatous; aligular surface epidermis with sclerotic cells forming patches and/or bands on lamina. Median leaves asymmetrical, lanceolate, up to 4.5 x 1.1mm, base oblique (obtuse-cuneate), apex long aristate (aristae up to two times the length of lamina), margins serrate; hypostomatous. Axillary leaves symmetrical, ovate to narrowly deltate, up to 5.0 x 1.8mm, base truncate to weakly subcordate, apex acute, margins of basal half serrate, apical half entire; hypostomatous; aligular surface epidermis with sclerotic cells forming patches and/or bands on lamina. Strobili bilateral, resupinate, up to 5 mm long, with two sporangial arrangements: (i) cone wholly microsporangiate; (ii) with the dorsal side containing both megasporangia and microsporangia randomly arranged and the ventral side wholly microsporangiate. Sporophylls dimorphous. Ventral sporophylls subpanduriform-ovate, up to 2.4 x 1.0mm, base obtuse, apex acute, margins serrate-entire to aculeate-entire, with a complete sporophyll-ptyx at the adaxial surface; amphistomatous; sporophyll-ptyx with serrate margin. Dorsal sporophylls lanceolate, up to 1.2 x 0.6 mm, base obtuse, apex cuspidate to aristate (aristae up to same length as lamina), margins serrate; hypostomatous. Megasporangia ovoid-triangular, with similar-sized spores; megaspores 210-(M200)-255µm in equatorial diameter, trilete, sub-globose, both proximal and distal surfaces rugulose. Microsporangia ellipsoid to roundish; microspores 15-(M19)-28µm in widest area, trilete, sub-triangular, both proximal and distal surfaces granulose to foveolate.

This species is closely allied to *S. squarrosa* Bak. from which it is distinguished by its serrate-margined leaves, very long aristate median leaves (aristae up to twice the length of the lamina) and two sporangial arrangements of the strobili. *S. squarrosa* has leaves with entire margins, aristae of median leaves up to 1.5 times the length of the lamina and strobili with one sporangial arrangement.

Other specimen examined:

GABON. Kkan, NE Mela, Mont de Cristal, Halle & Villiers 4788 (K)

ACKNOWLEDGEMENTS

The author is grateful to Dr B.A. Thomas, Botany Department, National Museum of Wales, Cardiff, for constant encouragement and Mr A.C. Jermy & Dr. N.K.B. Robson, Botany

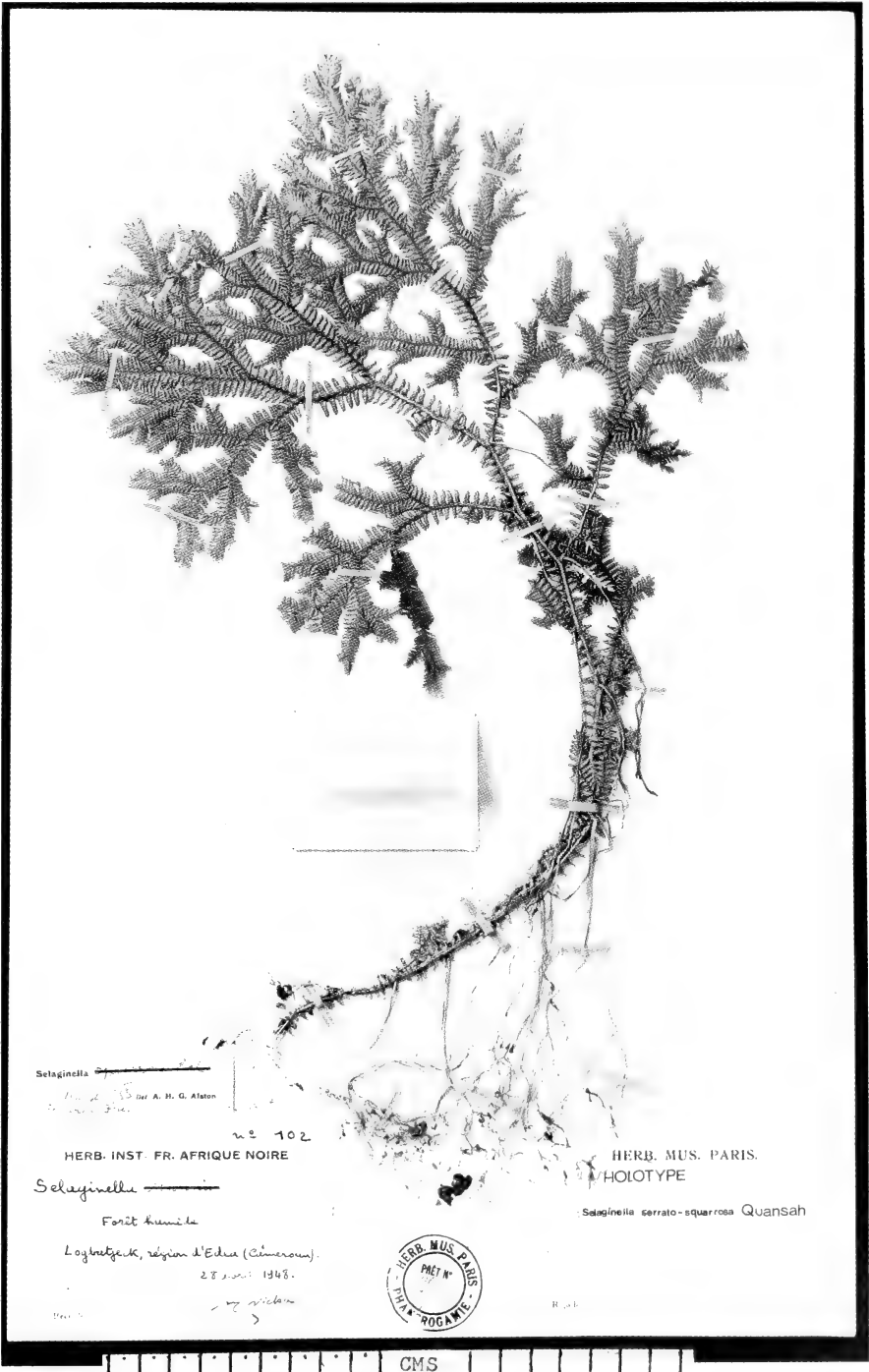


FIGURE 1. *Selaginella serrato-squarrosa* Quansah. Holotype (Nicklès 102, P) showing general habit. Photo: by permission by the Trustees of the British Museum (Natural History).

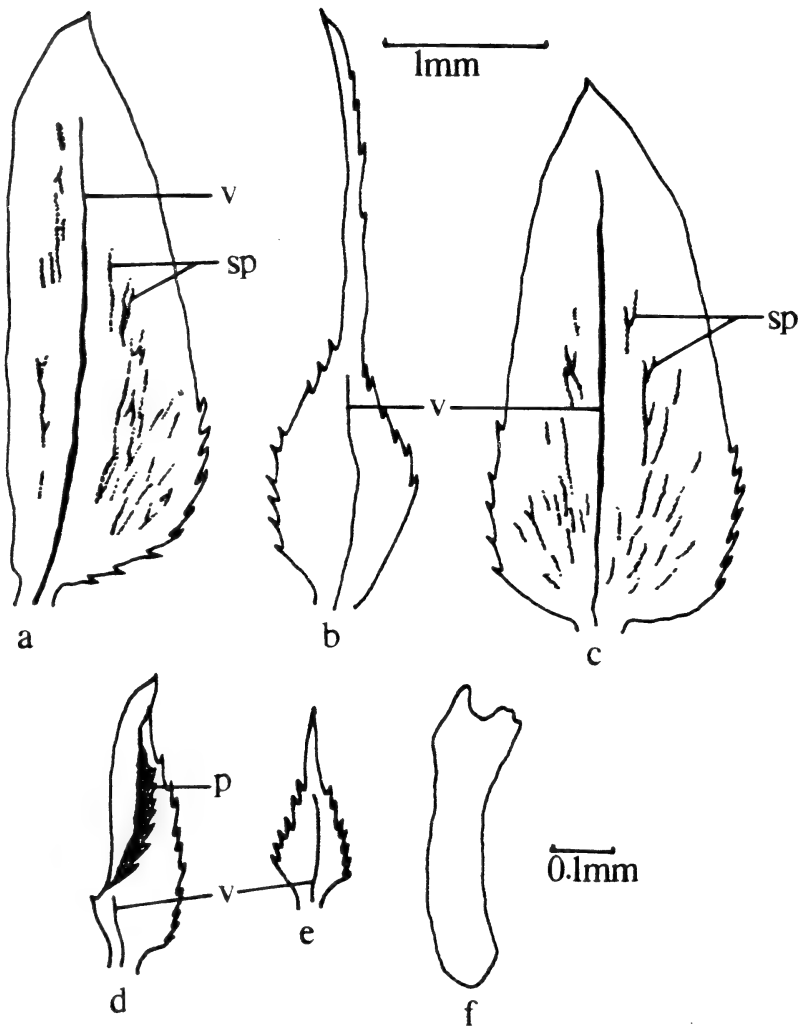


FIGURE 2. *Selaginella serrato-squarrosa*. a) lateral leaf; b) median leaf; c) axillary leaf; d) ventral sporophyll; e) dorsal sporophyll; f) ligule. a-e = 1mm scale; f = 0.1mm scale. p = sporophyll-ptyrux; sp = sclerotic patches; v = veins.

Department, British Museum (Nat. Hist.) for help with the Latin diagnosis. The main research, of which this publication is a part, was supported with a grant from the Ghana Government.

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NEW FERNS OF MADEIRA

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ABSTRACT

Three new endemic taxa from Madeira are described, *Hymenophyllum maderense* Gibby & Lovis, *Asplenium trichomanes* subsp. *maderense* Gibby & Lovis and *Ceterach lolegnamense* Gibby & Lovis; *Polystichum* × *maderense* Johnson and other endemic hybrids are discussed.

In the course of a study of the cytology of the fern flora of Madeira (Manton et al. 1986), some new ferns were discovered, and although the cytology of these new taxa has been described, they still require formal taxonomic description. In addition, another new hybrid has been found during the preparation of the forthcoming *Flora of Madeira*.

***Hymenophyllum maderense* Gibby & Lovis sp. nov.**

Habitu et textura *H. wilsonii* Hooker similis, praecipue venis segmentorum apice non attingentibus, cellulis laminariis brevioribus (ad duplo longioribus quam latioribus), minus regulariter dispositis, indusii ovatis, differt. Filix amphidiploidea, $2n = 62$. (Owing to the omission of the expression "sp." in the Alphabetical List of Taxa with data given in Manton et al. 1986, the chromosome counts for *H. maderense* appear to be attributed therein to *H. wilsonii*).

Holotypus: ex hort. Leeds, 1973, origin: Madeira, Queimadas, from a rock face in a gully below a levada, coll. J.D. Lovis s.n. 25 July 1970. BM (Fig. 1)

Mat-forming perennial with slender branched rhizomes bearing thin translucent fronds. Fronds 1.5 - 9.0cm in length, deep olive-green, oblong to oblanceolate in shape, pinnately divided, but sometimes with one or more lower pinnae much longer and more divided than the rest, giving a branched appearance; pinnae divided into 2 - 5 segments, segments broadest at the middle and about twice as long as broad; segmental vein terminates 4 cells short of end of pinna segment; lamina cells up to twice as long as broad, arranged haphazardly, each cell containing many (c. 80) chloroplasts, each chloroplast c. $5\mu\text{m}$ in diameter. Sori appearing stalked, inserted perpendicularly to the plane of the lamina; indusial valves spreading apart at maturity, ovoid, not tapering markedly at the apex, margins entire. Spores c. $55\mu\text{m}$ in diameter (range 53-57). $2n = 62$.

H. maderense is similar to *H. wilsonii* Hooker, but can be distinguished as the vein of the pinna segments stops short of the apex, the lamina cells are shorter and arranged haphazardly (as in *H. tunbrigense* (L.) Sm.), not in rows lying at an angle to the vein, and the indusial valves are ovate, not flask-shaped, and tapering markedly to the apex as in *H. wilsonii*. *H. maderense* is very rare in Madeira, being recorded only from a rock face and the side of a levada at Queimadas. However, the occurrence of hybrids of *H. maderense* × *H. wilsonii* (see below) indicates that it must once have been, and possibly still is, more widespread. Cytological evidence indicates very clearly that it is a markedly dibasic allopolyploid, derived by chromosome duplication from a hybrid of *H. tunbrigense* ($2n = 26$) × *H. wilsonii* ($2n = 36$).

Hybrids of *H. maderense* × *H. wilsonii* have been discovered at Queimadas and at Pico do Tapeiro. These plants are very close to *H. wilsonii* in morphology, and can be distinguished only by their different chromosome number ($2n = 49$), an irregular meiosis and bad spores.

***Asplenium trichomanes* subsp. *maderense* Gibby & Lovis subsp. nov.**

Habitu et textura *A. trichomanes* subsp. *quadrivalens* similis, praecipue frondis perviridibus subnitidis in statu vivo differt. Sporae 35 - $40\mu\text{m}$ longae. Filix hexaploidea, $2n = 216$.

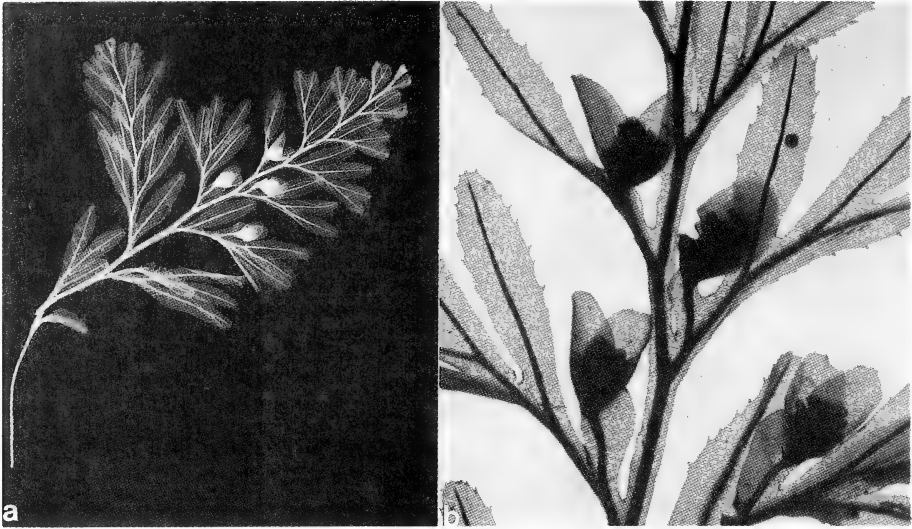


FIGURE 1. *Hymenophyllum maderense*, cult. Leeds 1973. A, whole frond x 1.3; B, portion of frond showing sori x 4.

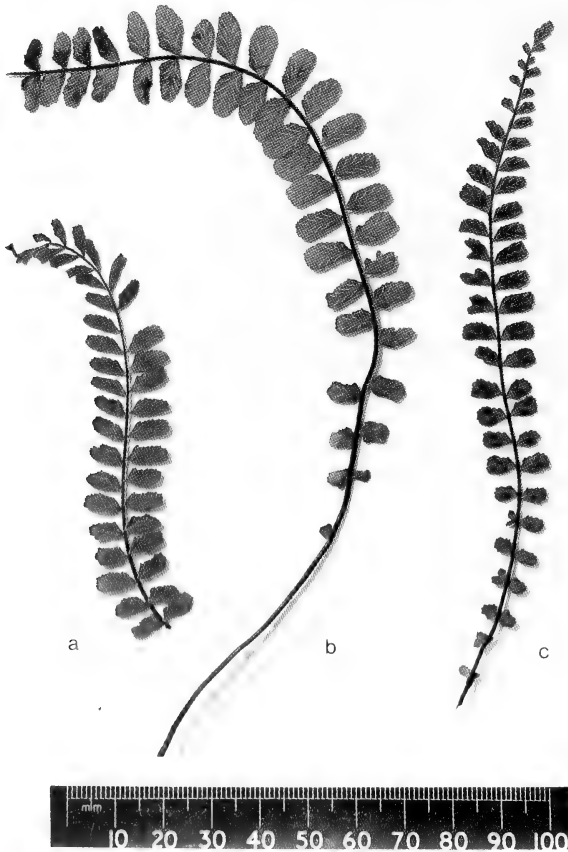


FIGURE 2. *Asplenium trichomanes* subsp. *maderense*, A & B wild collections; C ex cult. Leeds.

Holotypus: Madeira, Pico do Ferreiro, in a horizontal rock crevice, c. 1400m alt., coll. J.D. Lovis s.n., 26 July 1970. BM (Fig. 2).

Between *A. anceps* and *A. trichomanes* subsp. *quadrivalens* in morphology, but much closer to the latter taxon, from which it can usually be distinguished in fresh condition by darker green, sub-shiny pinnae. Spores 35 - 40µm long, rhizome scales < 4.5mm, narrowly lanceolate to subulate, with broad occluded central stripe. Hexaploid, $2n = 216$, endemic to Madeira.

Asplenium trichomanes subsp. *maderense* is believed to be an allopolyploid, derived from a hybrid of *A. anceps* and *A. trichomanes* subsp. *quadrivalens* by chromosome duplication. In addition to the type locality, it has also been discovered on Pico do Ariero c. 1800m alt. (coll. R. & W. Jäger, 15 March 1981).

***Ceterach lolegnamense* Gibby & Lovis sp. nov.**

Filix inter *C. aureum* (Cav.) L.v. Buch var. *aureum* et *C. aureum* var. *parvifolium* Benl & Kunkel magnitudine intermedia, frondis plerumque 9 - 24cm longis, 1.5 - 3.8cm latis, sporis (33-) 35-42 (-45)µm longis (perispore exclusus), numero chromosomatorum ($2n = 216$) magnitudine intermedius; distributi geographica differt.

Holotypus: Madeira, Serra d' Agua, coll. J.D. Lovis s.n. 4 April 1969. BM (Fig. 3)

The name *lolegnamense* is derived from an old name for Madeira (cf. Cossart 1984, pp. 2-4).

Differs from *Ceterach aureum* (Cav.) L.v. Buch var. *aureum* and var. *parvifolium* Benl & Kunkel in size, with fronds usually from 9 - 24cm long and 1.5 - 3.8cm wide, in spore size, (33-) 35 - 42 (-45)µm (excluding the perispore), chromosome number, $2n = 216$, and geographical distribution, being endemic to Madeira.

It has been suggested (see Manton et al. 1986) that *C. lolegnamense* is derived by hybridization between *C. aureum* var. *aureum*, a tetraploid taxon ($2n = 144$), and *C. aureum* var. *parvifolium*, an octoploid ($2n = 288$). *C. lolegnamense* is intermediate between these two taxa in size, spore size and chromosome number, but is confined to Madeira, whereas *C. aureum* var. *aureum* and *C. aureum* var. *parvifolium* are known only from the Canary Islands. Cytogenetic studies are in progress to confirm the relationship of the three taxa, and it is intended that the two taxa from the Canary Islands will be recognised at specific rank (Reichstein & Vida, pers. comm.).

***Polystichum* × *maderense* Johnson**

Holotype; Madeira, Rabaçal, G.C. Joad s.n. February 1866 K (Fig. 4)

Polystichum maderense Johnson (1866) was described from two or three

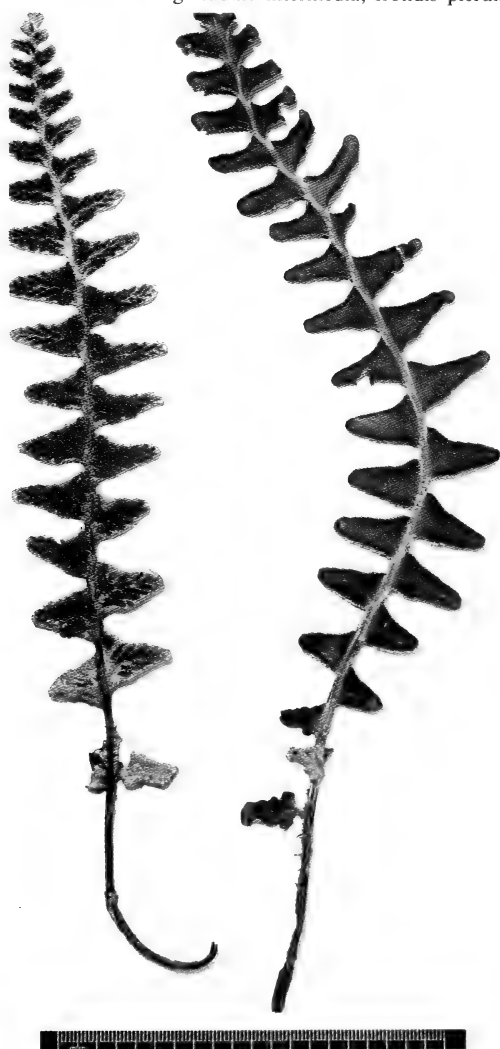


FIGURE 3. *Ceterach lolegnamense*, part of holotype.

fronds of a single specimen collected by G.C. Joad at Rabaçal, at the head of the Ribeira da Janela; Johnson was of the opinion that this fern was 'exactly intermediate between *P. falcinellum* Presl and *P. angulare* Presl' [= *P. setiferum* (Forssk.) Woytar] (Johnson 1866). In April 1969 J.D. Lovis, in the company of T. Reichstein and P.G.J. de Joncheere, found a hybrid at Rabaçal with morphology intermediate between *P. falcinellum* and *P. setiferum*, which he subsequently found to be pentaploid ($2n = 205$), thus confirming the proposed parentage of *P. falcinellum* ($2n = 328$) \times *P. setiferum* ($2n = 82$). In June 1969 M.L. Nilsson discovered a plant with similar morphology on Pico do Ariero, and that was determined as *P. maderense* by Hansen (1970). Unfortunately only a single sterile frond collected by Joad is at Kew (although in his description Johnson refers to the arrangement of the sori and shape of the indusia), and the Nilsson specimen at Copenhagen has shed all its spores. Therefore the hybrid nature of this fern can be confirmed only in the Lovis collection, but morphologically all these specimens are very similar and clearly represent the same taxon, the correct name for which must be *P. \times maderense* Johnson. Like *P. falcinellum*, *P. \times maderense* is a Madeiran endemic.



FIGURE 4. *Polystichum* \times *maderense*, holotype.

At the end of his account of *Aspidium*, Milde (1867) refers to *P. maderense* and suggests it may be the same as *Aspidium falcinellum* var. *subbipinnata* Moore. The varietal name var. *subbipinnata* appears not to have been published by Moore – Menezes (1914) refers to var. *subpinnatum* (sic!) Milde. Because the note by Milde follows his account for *Aspidium frondosum*, Romariz (1953) includes in the synonymy of *P. maderense* '*Aspidium frondosum* var. *subbipinnata* Moore in Milde?; *P. falcinellum* var. *subbipinnata* Moore?'. However, a specimen at Kew from the herbarium of Thomas Moore labelled in Moore's handwriting '*Polystichum falcinellum* var. *bipinnatum*, Hort. Veitch 1856, ex Madeira', is similar in morphology to *P. × maderense*. The following description is based on all the specimens studied:

Fronds coriaceous, up to 80cm. Stipe c. 1/3 length of frond, rhizome and lower part of stipe covered in brown triangular scales with a dark central stripe, scales higher up stipe and on rachis more sparse, concolorous, lanceolate with tapering points. Lamina oblanceolate – lanceolate, pinnate, pinnatifid, but bipinnate at base of lower pinnae; pinnae lanceolate but with innermost apiscopic segment enlarged, pinna segments cut 1/4 to 1/2 width of the pinnae, not overlapping, slightly toothed, tapering to a distinct apical spine. Indusium > 1mm, peltate with central dark spot, margin irregularly toothed with a few multicellular hairs. Spores abortive. $2n = 205$.

Another *Polystichum* hybrid is known only from three herbarium sheets at Kew, and may well have existed as a single hybrid plant. One specimen from Camacha, Madeira was collected by Miss Ellen Taylor s.n. 19 December 1865, from 'a single plant growing



FIGURE 5. *Polystichum falcinellum* × ?, Taylor s.n., 19 Dec. 1865.

in a bed of *Nephrodium falcinellum*' (Herbarium of Revd R.T. Lowe) (Fig. 5). A further specimen was collected by Revd G.N. Burningham, and, as stated in a letter (22 September 1875) from Burningham that is attached to the sheet, 'was growing amongst many plants of *Aspidium falcinellum* in Madeira, and which Mr Lowe when last in Madeira thought might prove a distinct species'; the third specimen has no collector's label, but may be a further Burningham specimen.

This hybrid certainly has *P. falcinellum* as one parent as it has a coriaceous lamina, and similar indusia. The identity of the second parent is much more difficult; the only other *Polystichum* species on Madeira are *P. setiferum* (which seems unlikely as *P. setiferum* \times *P. falcinellum* is the parentage of *P. maderense*, and *P. maderense* differs in that it does not have rounded, crowded or overlapping pinnules) and the endemic *P. drepanum* (Sw.) C. Presl [it would be surprising if *P. drepanum* were to be the second parent for two reasons:- first, it is most unlikely that this very rare species which is now confined to a high valley in north-west Madeira was ever growing naturally in the region of Camacha, and secondly, since the combination of *P. falcinellum* and the diploid *P. setiferum* produces *P. maderense*, it is not likely that the Camacha hybrid, with its generally similar form, could be the combination of *P. falcinellum* and *P. drepanum*, because the latter is a tetraploid species with a markedly triangular frond and very open pinnation]. The third possibility is that the second parent is an as yet unknown, probably diploid, very likely extinct species of *Polystichum*. Because of the rarity and uncertain origin of this hybrid we refrain from giving it a name, but it is described below:

Polystichum falcinellum \times ?

Fronds coriaceous, up to 100cm long. Stipe c. 1/3 total frond length, green; rhizome and stipe base not seen; stipe sparsely covered and rachis more densely covered with brown lanceolate scales with tapering points. Lamina oblanceolate, up to 16cm wide, pinnate, pinnatisect; pinnae tapering, pinnules symmetrical about pinna axis except for innermost acroscopic pinnule which is always larger than its neighbour; pinnules up to 8mm long (innermost acroscopic pinnule up to 14mm), crowded with innermost pinnules overlapping, ovate, toothed and with apical spine. Indusia 1mm, peltate with small central dark spot, margin irregularly toothed. Spores abortive.

Madeira, Camacha, a single plant growing in a bed of *Nephrodium falcinellum*, Miss Ellen Taylor s.n. 19 December 1865. Herbarium of Revd R.T. Lowe. K (Fig. 5).

ACKNOWLEDGEMENTS

We thank Dr N.K.B. Robson who assisted with the latin diagnoses, A.C. Jermy for advice, Prof. T. Reichstein and Prof. G. Vida for information regarding their studies on *Ceterach* in the Canary Islands, and Dr W. Jäger for loan of his example of *Asplenium trichomanes* subsp. *maderense* collected on Pico do Ariero.

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THE ECOLOGY AND DISTRIBUTION OF PTERIDOPHYTES OF ZOMBA MT., MALAWI*

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ABSTRACT

Ninety-six species of pteridophytes are known from the Zomba area, from the earliest collections of the Livingstone Expedition, 1859, up to recent collections by the author from 1980-86. Distributional data is given for the pteridophytes of Zomba Plateau (altitude 1500-2085m) with species in remnants of undifferentiated Afromontane forest and grassland, riverine forest and plantations of introduced conifers, and the pteridophytes of the mountain slopes (1000-1500m) from the rocky cliff-edges, the *Brachystegia*/mixed woodlands and the plantations of the lower slopes. Very few pteridophyte species are found below 900m altitude in the surrounding savanna areas. Some species from earlier collections, e.g. 1896 (Whyte), 1967 (Berrie), have not been seen recently from 1980-86 and may no longer be present in the Zomba area.

INTRODUCTION

The earliest European exploration of Central Africa by the Livingstone Expedition passed through the Zomba area in September 1859 (Baker 1959, Jackson 1959). The plants collected then included a small number of pteridophytes (12 species in 10 genera) among the very many numbers of other plant groups (Burkill 1897, 1898 & 1906). Later collectors in special expeditions also only included a few pteridophytes e.g. the Brass collections of the Vernay Nyasaland Expedition of 1946, with 33 pteridophyte numbers (27 species in 17 genera) out of the 288 numbers of all plant groups from the Zomba area (Ballard 1953, Brass 1953). Schelpe (1970) in *Flora Zambesiaca* listed only 21 species, in 14 genera, for this area. The most recent checklist of the pteridophytes of Zomba Mt. (Berrie 1984) included 93 species in 43 genera.

The present paper discusses the distribution of 95 pteridophyte species in 45 genera presently or previously recorded for the Zomba area.

STUDY AREA

Location

Zomba mountain lies east of the Great Rift Valley of Central Africa, in the Southern Region of Malawi. At latitude 15°10' - 23°S and longitude 35°15' - 23°E it is the highest part and the most northern inselberg of the Shire Highlands. This ridge of highlands runs NE - SW between Lake Chilwa to the east and the Shire River to the west (Figure 1a).

The Zomba mountain massif consists of two plateau areas separated by the Domasi River, flowing almost due east between the northern Malosa Plateau and the Southern Zomba Plateau (Figure 1b). Both plateaux are forest reserves. Zomba Plateau is 8km N-S and 12km E-W, with a narrow road on the southern scarp from Zomba town at its base. There are many small roads around and through the conifer plantations on Zomba Plateau, interconnected by narrow footpaths. Malosa Plateau is larger, 14km N-S and 10km E-W, with no road up its very steep scarp, no regularly used pathways over or around it, and only a few trial plots of exotic conifers planted there. Due to its inaccessible nature and the limitation on time available for fieldwork the Malosa Plateau was not included in the present study. Reference to Zomba Mt. in the text thus includes Zomba Plateau, the south-west and south-eastern slopes, Zomba town area at the southern base of the mountain, and Zomba District the area around the mountain massif.

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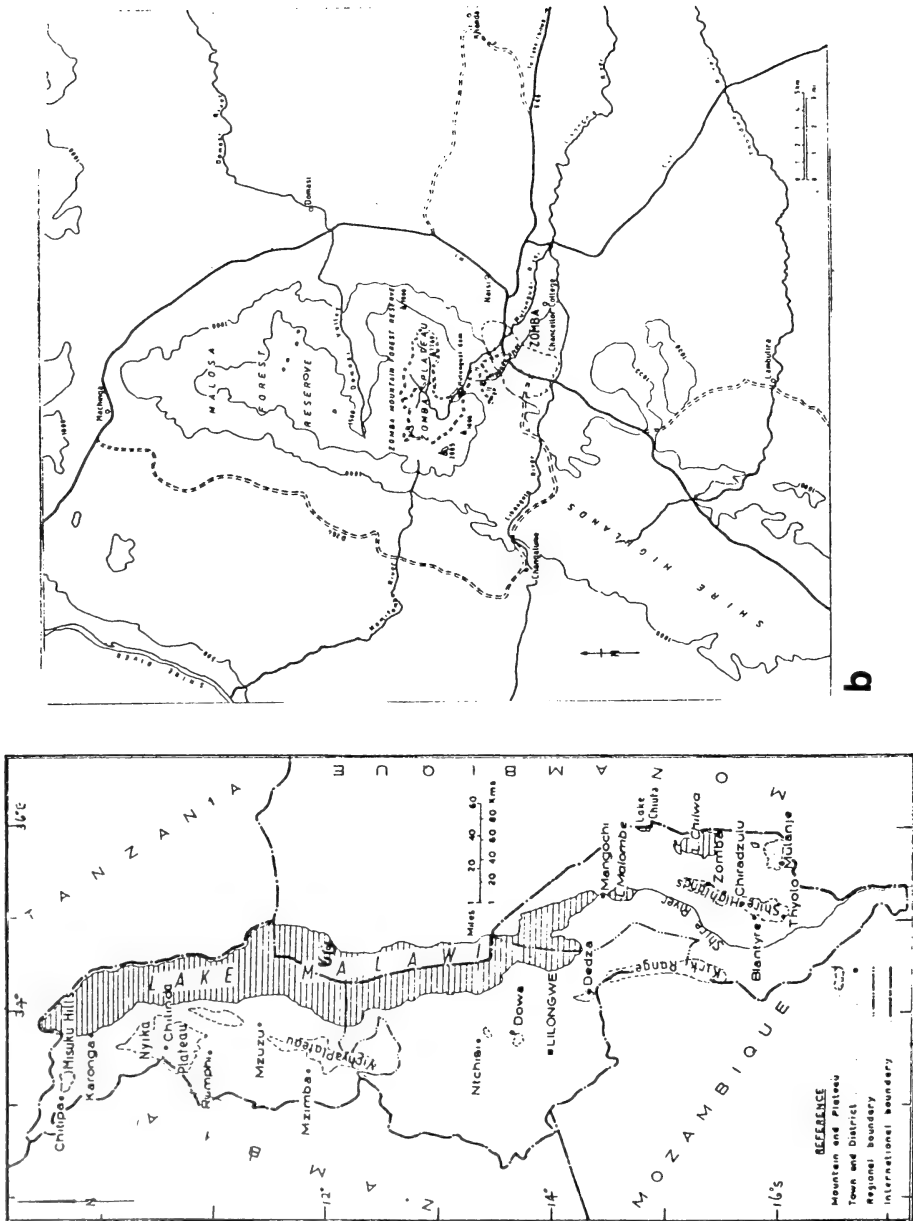


FIGURE 1. a) Map of Malawi showing position of Zomba at the northern end of the Shire Highlands; b) The Zomba mountain massif and Zomba District. (Modified from Berrie 1984)

General vegetation

Malawi is within the floristic region or phytochorion known as the Zambesian Region in High Africa (White 1983). On the "Vegetation Map of Africa" (UNESCO/AETFAT/UNSO, White 1983) Zomba mountain is shown as a tiny island of 'undifferentiated montane vegetation, (a) Afromontane', No. 19 in the series Forest Transitions and Mosaics (No. 11-24). This small area, 19a, is surrounded by 'wetter Zambesian miombo woodland (dominated by *Brachystegia*, *Julbernaldia*, and *Isoberlinia*)', No. 25 in the Woodland Series (No. 25-30).

Zomba Plateau has a number of vegetation types including small areas of montane grassland, a few isolated patches of montane forest, and riverine forest along the main Mulunguzi River valley and a few streams. The largest areas of conifer plantations are *Pinus patula* Schlecht. & Cham. with other older trial plots of exotics, mainly conifers, and a few of the indigenous conifer *Widdringtonia nodiflora* (L.) Powrie (Mulanje Cedar).

The Afromontane vegetation of Zomba Plateau includes grassland along the western rocky ridges from about 1800-2085m. The rough grassland with small shrubs and scattered herbs has species of *Protea*, *Xerophyta* (*Vellozia*), *Vernonia*, *Senecio*, *Helichrysum*, and

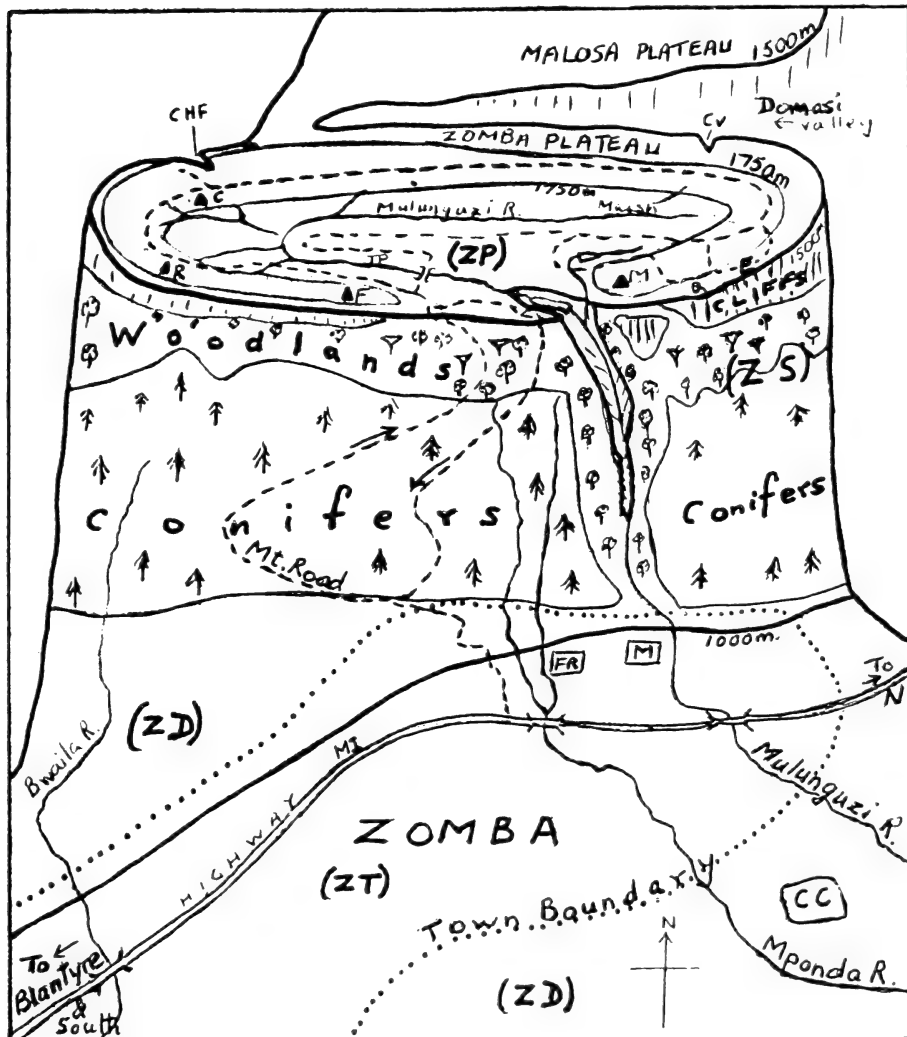


FIGURE 2. Diagrammatic representation of Zomba Mt. showing the altitudinal areas of Zomba Plateau (ZP), Zomba slopes (ZS), Zomba town (ZT), and Zomba District (ZD). (Abbreviations: Peaks on Zomba Plateau: R = Radiomast and Malumbe Peak (2085m); C = Chiradzulu Peak (2050m); F = Nawimbe Firetower (1800m); M = Mulunguzi Peak (1769m). Lookouts: Q = Queen's View; E = Emperor's View. TP = Trout Ponds. CHF = Chingwe's Hole Forest. CV = Chivunde valley. In Zomba town, FR = Forestry Research Institute of Malawi (F.R.I.M.); M = The National Herbarium of Malawi (MAL). CC = Chancellor College, University of Malawi.

Plectranthus. The tussocky grasses are dominated by species of *Andropogon* and *Exothea*, while the forest/grassland marginal areas have tall plants of *Hypericum* sp. and shrubs of *Philippia benguelensis* with Bracken, *Pteridium aquilinum*, dominant in this transitional zone. The northern and eastern rims of the high plateau are almost completely planted with *Pinus patula*, except for remnants of riverine forest in strips along the smaller Mulunguzi tributaries. A very narrow fringing plantation of *Eucalyptus* sp. is along the southern rim, almost at the cliff-edge, around Mulunguzi peak (1769m) near the Lookout area, about 750m above Zomba town (Figure 2).

The remnants of Afromontane forest on Zomba Plateau are found at the heads of small valleys, hanging at the cliff-edges, with small streams falling to the main valleys below, as at Chingwe's Hole Forest (1900 alt.) facing NNW. The stream here forms the headwaters of the Namitembo River, flowing westwards to the Shire River. Similar remnant forest is found where the Chivunde stream begins, flowing due north to join the Domasi River in the valley below.

Chingwe's Hole (montane) Forest, Figure 3, includes very many tree species evenly spread throughout a very small area with phorophytes ('host trees') for epiphytic ferns including *Podocarpus latifolius*, *Myrica salicifolia*, *Nuxia congesta*, *Cassipourea congoensis*, *Diospyros whyteana*, *Ilex mitis* and *Xymalos monospora*. A few genera of trees found here (*Halleria*, *Ilex* and *Nuxia*), have the same species along the river but one genus, *Syzygium*, has one species in the montane forest (*S. guineense* subsp. *afromontanum*) and another (*S. cordatum*) in the river forest. *Halleria lucida* is found usually at the montane forest margins and occasionally in small clumps on the nearby grassland, but along the river it is very abundant and bears the greatest number of epiphytic ferns, of most species, in the riverine forest.

Riverine forest occurs along the Mulunguzi River and its smaller tributaries on Zomba Plateau, and extends downriver from the Mulunguzi Dam at the plateau rim, about 1450m alt., into the deeply cut valley below as far as the top of the gorge, at approximately 1380m. Even on the Plateau the riverine forest is mostly a fringing forest. There are a few dense forest patches where *Ilex mitis* and *Rauvolfia caffra* bear filmy ferns and other epiphytes, but along the river banks there are smaller trees, of *Halleria lucida* and *Syzygium cordatum* bearing many epiphytes on the trunks and branches, but not the filmy fern masses of the closed forest.

The very steep slopes above the Gorge and the exposed rocky edges of the Plateau have a rather open woodland of *Brachystegia*/mixed species. Only a few epiphytic ferns occur here on trees of *Julbernaldia globiflora*, *Heteromorpha arborescens*, *Parinari curatellifolia* and *Brachystegia* spp. The very occasional trees of, Fig. 4, *Acacia sieberana* scattered on the upper mountain slopes carry a very heavy load of fern epiphytes. The cliff-faces on the southern scarp stand out above the very stunted woodland at their lower edges, about 1300m alt. The same tree species are here very small, sometimes only 2-3m in height, and rarely with any epiphytic ferns though they sometimes have an occasional orchid present. The conifer plantations, Fig. 5, of the lower slopes are mostly *Pinus patula*, with a small amount of *Cupressus* sp., stretching from the town boundary at 1000m up to the stunted woodland at the cliff-base. Below the 1000m level, within and around Zomba town, the land is highly cultivated with Maize and other crops except along the streams and the Mulunguzi River. Remnants of riverine forest include some large forest trees like *Khaya nyasica* and *Filicium decipiens* even in the town area. Away from permanent streams there are not many places where pteridophytes can survive. Some of the very dry rocky outcrops on the lower slopes of the mountain and at some distance from its base have poikilohydrous, xerophytic ferns only seen easily during the wet season. The open savanna areas surrounding the mountain have very little uncultivated land. Only streamsides and water channels support any vegetation in which pteridophytes may be found. The Mulunguzi



FIGURE 3. Montane epiphytes in Chingwe's Hole Forest (altitude 1900m) on Zomba Plateau. On *Myrica salicifolia*, 1½ - 2m from ground level, there are small narrow pendant fronds of *Asplenium sanderstonii* (centre and lower branch) with proliferating frond tips, and the larger spreading fronds of *Arthropteris monocarpa* projecting from long creeping rhizomes closely attached to the tree trunk. (photo: G.K. Berrie)



FIGURE 4. Woodland on upper slopes of Zomba Mt. (altitude 1450m). Epiphytes on the spreading branches of *Acacia sieberana*, many ferns and a few orchids. Dominant ferns are *Pleopeltis excavata* and *P. macrocarpa* with scattered plants of *Asplenium aethiopicum* and *A. theciferum*.

R. is permanent but many of the smaller streams dry up completely during some part of the year. Thus the vegetation of Zomba Mt. while going through severe conditions during the dry season appears always green, but below the 1000m level, months of dry season change the appearance of the land around the mountain, each year.

Climate

The climate of Malawi is the Tropical Summer Rain, type II, of Walter (1971), with the wet summer season of the southern hemisphere from November to April and the dry season from May to October.

However, the dry season can be divided into the cool, early dry season months and the later, hot to very hot, months. In Zomba the coldest months are usually June/July (minimum 6°C) while the hottest months are Sept./October (maximum 34°C). Frosts have not been recorded for Zomba town, or at Chancellor College (CC) where meteorological records have been taken since 1972, but frost damage to tree ferns (*Cyathea* sp.) has been seen on Zomba Plateau (ZP), at 1500m and 1800m, on a number of occasions during late June/early July in recent years between 1980-86.

Continuous temperature records are not available for Zomba Plateau but some data (F.R.I.M.) for 1978-80 can be compared with that for Chancellor College (CC.: Geog. Dept.), as follows (in °C):

	Abs. max.	Abs. min.	Range		Abs. max.	Abs. min.	Range
ZP. (1900m) dry season:	28	4	24	wet season:	27	11	16
C.C. (900m) dry season:	34	6	28	wet season:	33	11	22

Rainfall data for both places for the ten year period 1976-86 gives a mean annual total for ZP as 2244mm and for CC as 1464mm. If a dry month is one with less than 25mm then the dry season may be given as 5 months (May - Sept.) or 6 months (May - Oct.) since October rainfall varies from 0 - 132mm on ZP and from 0 - 72mm at CC in different years.

An additional factor in climate is the frequent mist and cloud-cover on the mountains. The cloud base may extend down to the 1000m level at the base of the mountain, around the edge of Zomba Town. During some wet season months (Jan. - March) there may be 10-13 complete days like this; in dry season months (June - Sept.) there may be 6-8 days per month like this, or for most of the morning only. Looking up to Zomba Mt. from Chancellor College in the dry season (Aug.) the very early morning sky (5.30-6.30 am) may be clear all around the mountain, but low heavy clouds come across from the eastern end, from over Lake Chilwa, so by 7 am the Plateau is enveloped in thick cloud. This may remain to 10 am or midday. This 'condensation cloud' must add considerably to available water, especially for the epiphytes on the Plateau and upper slopes, at a time when measured rainfall is zero or nearly so. Cloud cover can also change very rapidly during the wet season, giving heavy isolated local rain, e.g. on the lower slopes near the Herbarium but none in Zomba town centre about 1km away, or at Chancellor College 1.5km lower down the slope.

This pattern means that the climate controls the seasons but the local weather conditions control the rainfall, so the weather as much as the climate affects the plant distribution.



FIGURE 5. Marginal habitat: edge of *Pinus patula* plantation on Zomba Plateau (altitude 1550m). Ground flora dominated by *Nephrolepis undulata* with occasional *Dryopteris inaequalis* var. *inaequalis* (centre), *Arthropteris monocarpa* in more shaded parts spreading up the lichen-encrusted trunks of *Pinus*. (photo: A. Berrie).

OBSERVATIONS ON THE DISTRIBUTION OF THE PTERIDOPHYTES

Habitat

Most pteridophyte species are not restricted to one vegetation type, i.e. to montane grassland, montane forest, riverine forest, woodland or the plantations described. Instead they occur in similar habitats within and around these areas. Here I have grouped the pteridophytes by habitat, from wet to dry; from the permanently wet, closed forest type (montane), the permanently moist, closed forest (riverine), to the remnant riverine forest, and the woodland habitats. These are listed as Forest/woodland species in Habitats I - VI (Table 1). Other permanently wet, non-forest habitats include riversides, marshlands and swamps (Habitat VII). The seasonally very wet habitats are VIII: seasonal pools, and IX: seasonal flush areas on rocky outcrops. The remaining habitats are not particularly wet and are without closed tree-cover, but may be found at edges of various forest types and in more open places. These are X: marginal habitats, XI: sheltered habitats, and XII: exposed habitats.

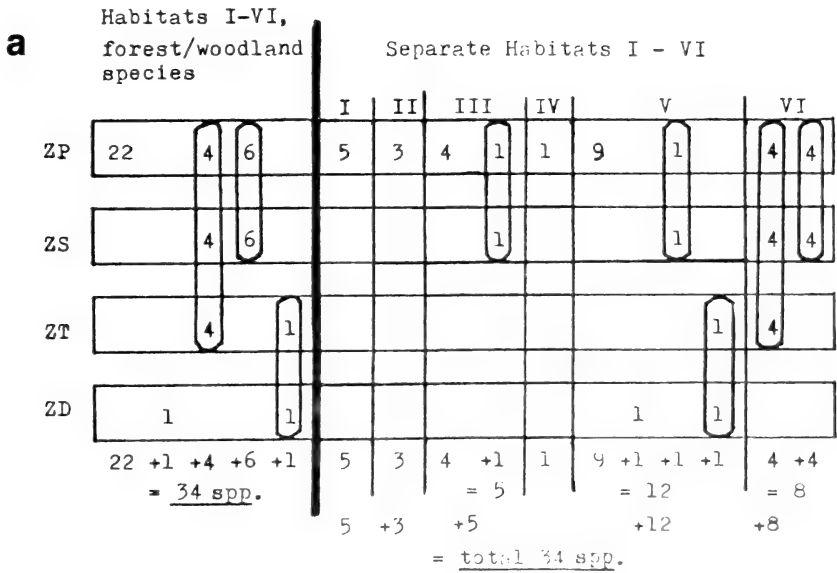
Altitude

Table 1 lists the distribution of the pteridophytes in these Habitats, 1-XII, in each altitudinal area, with details of habit and habitat of each species. The whole area was divided into four altitudinal zones as follows:

- 1. Zomba Plateau (ZP), all above 1500m alt. up to 2085m; and the area around the Mulunguzi Dam, at approximately 1450-1500m;
- 2. Zomba slopes (ZS), the mountain slopes from 1000-1500m;
- 3. Zomba town (ZT), the inner town area, approximately 900-1000m;
- 4. Zomba District (ZD), the lower slopes and surrounding area within the administrative boundary of Zomba District, down to 650m alt.

Some species are restricted to each of these four areas, to ZP, ZS, ZT, or ZD. Others have wider distribution, so combinations of these areas give continuous distribution of species in ZP,ZS,ZT,ZD; ZP,ZS,ZT; ZP,ZS; ZS,ZT,ZD; ZS,ZT; and ZT,ZD; while discontinuous distribution occurs in ZP,ZS,ZD; ZP,ZT,ZD; and ZP,ZT.

This altitude zonation is used in the distribution diagrams showing combinations of Habitats and altitude in Figure 6.



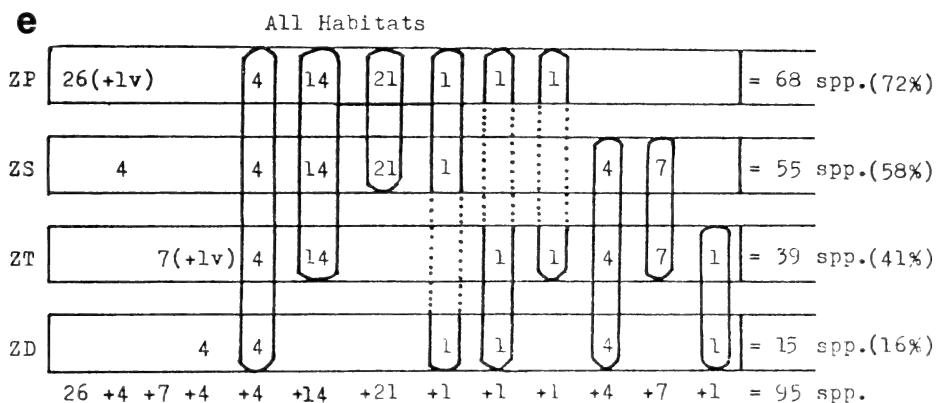
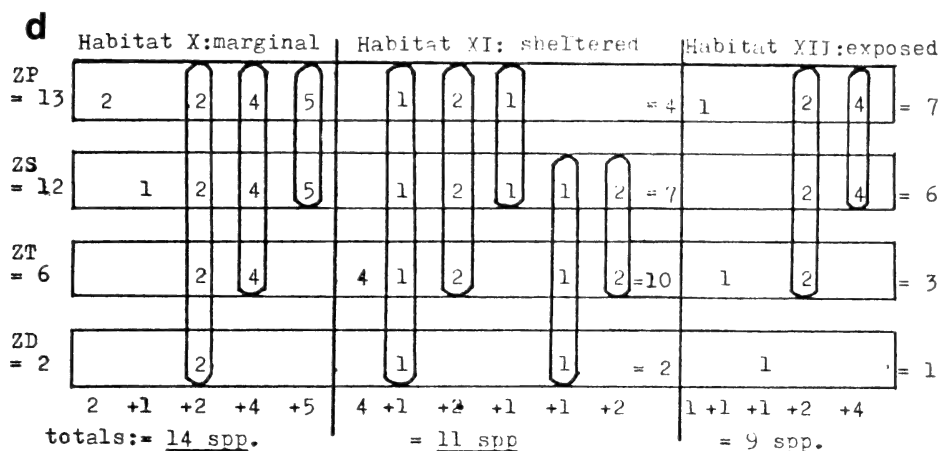


FIGURE 6. Distribution of pteridophyte species in Habitats I-Xii in altitudinal zones (ZP, ZS, ZT, ZD) showing restricted, continuous and discontinuous patterns: a) forest/woodland species (Habitat I-VI); b) same in different forest types; c) non-forest, permanently wet, riversides (Habitat VII); seasonal pools (VIII); and seasonal flush (IX); d) marginal (X); and seasonally extreme, sheltered (XI) and exposed (XII); e) species in all habitats.

TABLE 1

Distribution of the pteridophytes by habitat and altitude. The altitudinal areas in each Habitat are separated by a dotted line; the Habitats are separated from each other by a solid line. See text for abbreviations. Taxa not seen during this study (1980-1986) are marked with an asterisk*

Nomenclature follows *Flora Zambesiaca* (Schelpe 1970) except for the family Thelypteridaceae which follows Holttum (1974) in the recognition of more genera.

(1) Habitats I-XII Area, and species	(2) Local distribution habit and Regional distrib.	(3) Plant habit and habitat
<hr/>		
I: montane forest only (ZP only: 5 spp. including 1 var.)		
ZP only = 5 spp.		
<i>Asplenium boltonii</i>	f : T/E Za.Zb.	Terrestrial in deep shade or low level epiphyte, to 1m on tree trunks.
<i>A. dregeanum</i>	r : T/E Za.Zb.M.SA	Terrestrial, or epiphyte on tree bases.
<i>Elaphoglossum acrostichoides</i>	r : E Zb.L.M.SA.	Epiphyte, on upper surface of branches, 2-3m from ground level.
<i>A. lobatum</i>	r : T Zb.M.S.SA.	Terrestrial, in deep shade near stream. One location only
<i>Dryopteris inaequalis</i> var. <i>atropaleacea</i> (see Habitat X for other var.)	r : T Za.	Large erect terrestrial, like a small tree fern, in deep shade; few scattered plants, one location only.
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II : montane and riverine forest, and cliff-edge forest (ZP only)		
ZP only = 3 spp.		
<i>Elaphoglossum spathulatum</i>	r : E/L Za.Zb.L.M.S.SA.	Epiphyte in montane and cliff-edge forest; lithophyte in riverine forest.
<i>Hymenophyllum polyanthos</i> var. <i>kuhnii</i>	a : E/L Zb.M.SA.	Pendant epiphyte, massed on tree trunks up to 3m, on vertical and horizontal surfaces; lithophyte near waterfalls; usually in deep shade.
<i>Oleandra distenta</i>	o to a : E/T/L Za.Zb.M.S.SA.	Epiphyte, becoming terrestrial from rooting of pendant rhizomes. Old erect rhizomes covered by lichens growing at cliff-edge; lithophyte at riverside.
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III : montane and riverine forest (ZP and ZS = 5 spp.)		
ZP only = 4 spp.		
<i>Asplenium mannii</i>	a : E Za.Zb.M.	Small creeping epiphyte; ground level to 4m, on large and small trees and lianes; often with <i>A. sandersonii</i> .
<i>A. megalura</i>	o : E Za.	Tufted epiphytes; small fronds (10-15 cm) at 1-3m from ground but much larger (to 40cm) at 6m and in higher branches.
<i>A. sandersonii</i>	a : E Zb.M.SA.	Spreading, low level epiphyte; 1-2m from ground.
<i>Trichomanes borbonicum</i>	o : E Zb.M.SA.	Tiny semi-erect filmy fern, low level epiphyte 1-2m from ground; usually with <i>Hymenophyllum polyanthos</i> .

III : montane forest (ZP) and riverine forest (ZP, ZS).
ZP, ZS = 1 sp.

<i>Belchnum giganteum</i>	f : T Za.Zb.L.M.S.SA	Large erect terrestrial; on open riverbanks and deeply shaded streams.
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IV : riverine and cliff-edge forest (ZP only)
ZP only = 1 sp

<i>Blechnum tabulare</i>	o : T Za.Zb.L.M.S.SA.	Erect terrestrial; in forest/woodland at cliff-edges and along streams.
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V : riverine forest only (ZP, ZS, ZT and ZD = 12 spp.)
ZP only = 9 spp.

<i>Blechnum attenuatum</i>	f to a : E Za.Zb.	Erect epiphyte on tree ferns (<i>Cyathea</i> spp.), ground level up to 2.5m.
<i>Lycopodium verticillatum</i>	o : E Za.Zb.L.M.S.A.	Epiphyte, on horizontal branches and tree trunks at angles up to 70° but not on vertical trunks; young plants erect, later bending; mature plants pendant.
<i>Blotiella natalensis</i>	r : T Za.Zb.M.S.A.	Large terrestrial, like a small tree fern, in deep shade, swampy area in wet season.
<i>Elaphoglossum hybridum</i>	r : T Zb.M.S.A.	Tufted terrestrial; on vertical earthbank at riverside, in deep shade.
* <i>Asplenium erectum</i>	s* Za.Zb.M.S.S.A.	21-7-62, Mwanza 2512 (MAL*), "on rocky riverbank".
* <i>A. linckii</i>	s* Zb.	1896, Whyte (K*) "Zomba Rock"
* <i>A. monanthes</i>	s* Zb.L.M.S.A.	1-4-80, Blackmore 1166 (MAL*), "streamside in dense forest"
* <i>A. pseudoauriculatum</i>	s* Zb.M.S.A.	28-5-46, Brass 16059 (K*, NY), "occasional on rocks in riverine forest"
* <i>Polypodium polypodioides</i> subsp. <i>ecklonii</i>	s* Zb.M.S.S.A.	21-1-67, Berrie 30 (K*), "epiphyte on tree branch over-hanging river".

V : as above
ZD : 1 spp

* <i>Pteris vittata</i>	s* Za.Zb.L.M.N.S.S.A.	5-4-80, Blackmore 1193 (K, MAL*), "by roadside in riverine forest dominated by <i>Khaya nyasica</i> ".
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V : as above
ZP, ZS = 1 sp.

<i>Selaginella kraussiana</i>	a : T Zb.M.S.S.A.	Creeping terrestrial, along riverbanks and masses in ground flora of forest.
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V : as above
ZT, ZD = 1 sp

<i>*Asplenium formosum</i>	s *	(ZT):8-7-62, Mwanza (MAL*), "rocky surface near River"
	s *	(ZD): 11-4-80, Blackmore and Morris 1223
	Za.Zb.M.	(MAL*), "riverbank in <i>Khaya</i> forest"

VI : montane forest (ZP), riverine forest (ZP, ZS), remnant riverine forest (ZP, ZS, ZT), and woodlands (ZS). (all areas = 8 spp.)
ZP, ZS, ZT = 4 spp.

<i>Asplenium theciferum</i> var. <i>concinnum</i>	a : E Za.Zb.M.SA.	Epiphyte, low and high levels, trunks and branches; in shade of forest, in open and closed woodland, occasionally on road-side trees (ZT).
<i>Pleopeltis macrocarpa</i>	f to a : E/L Za.Zb.L.M.S.SA.	Epiphyte, usually on upper surface and sides of branches, occasionally on tree trunks; lithophyte near river at lower altitudes (ZS, ZT).
<i>Loxogramme lanceolata</i>	f : E/L Za.Zb.M.SA.	Low level epiphyte in deeply shaded montane forest (ZP), and near river (ZP); lithophyte by river at lower altitudes (ZS, ZT).
<i>Asplenium aethiopicum</i>	f : E/T/L Za.Zb.L.M.S.SA.	Epiphyte on mid to high branches from 4-10m, in forest (ZP, ZS) and at riverside (ZP, ZS); on tree ferns (<i>Cyathea</i> , ZP), and cycad trunks (<i>Encephalartos</i> , ZT). T/L on ZS, ZT.

VI : as above
ZP, ZS = 4 spp.

<i>Pleopeltis excavata</i>	a : E/L Za.Zb.M.SA.	Epiphyte, on medium to high level branches on ZP, lower levels in woodlands (ZS); rarely lithophyte at lower altitudes (ZS).
<i>Pyrrosia rhodesiana</i>	o : E/L Zb.M.	High level epiphyte in montane forest (ZP), lower level epiphyte or lithophyte at lower altitudes, near rivers.
<i>Arthropteris monocarpa</i>	a : T/E Za.Zb.M.SA.	Terrestrial, becoming epiphytic; in shade of forest (ZP) and in open woodland (ZS), and outer parts of conifer plantations (ZP, ZS).
<i>Asplenium anisophyllum</i>	f : T Zb.M.S.SA.	Terrestrial, tufted but spreading; in general ground flora of montane forest (ZP), on steep banks of riverine forest (ZP), on rocky slopes of closed woodland (ZS).

VII : riversides, streambanks, marshlands and swamps (all areas = 20 spp.)
ZP only = 1 sp.

<i>Lycopodium carolinianum</i> (var. <i>affine/tuberosum</i> ?)	a : T Za.Zb.M.	Creeping terrestrial; montane grassland streamside, very marshy, with <i>Sphagnum</i> sp. (bog moss). Some plants with tubers.
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VII : as above
ZS only = 3 spp.

<i>Vittaria volkensii</i>	r (s) : E Zb.M.	Mid-level epiphyte, 3-4m from ground, on trunk and large branch (crown base) of <i>Parinari</i> tree near waterfall. First collection for Zomba: 28-5-85, Berrie 636 (MAL).
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<i>Cheilanthes farinosa</i>	r (s) : T Za.Zb.B.	Small terrestrial, in rock crevice at edge of woodland, 3m from river. First collection for Zomba: 28-5-85, Berrie 637 (MAL).
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* <i>Pteris dentata</i>	s* Za.Zb.L.M.SA.	31-12-81, Chapman & Patel 6029 (MAL*), "along streamside, close to water"
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VII : as above
ZT only = 1 sp

<i>Equisetum ramosissimum</i>	f to a : T Za.Zb.L.M.SA.	Terrestrial with spreading, deep underground rhizomes; along streambanks of lower mountain slopes; always in moist shady positions.
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VII : as above
ZP, ZS, ZT = 2 spp.

<i>Cyathea dregei</i>	a to r: T/A Za.Zb.L.M.S.SA.	Tree fern; terrestrial, but may stand in water at riverside; always very close to water; few by montane grassland stream, abundant by river (ZP); not in montane forest; rare on lower mountain slopes, one by river, ZT.
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<i>Tectaria gemmifera</i>	f to a : T Za.Zb.M.SA.	Large tufted terrestrial with very spreading fronds; along river-side paths (ZP), streambanks (ZS, ZT); always in moist shady places.
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VII : as above
ZP, ZS, ZD = 1 sp.

<i>Osmunda regalis</i>	a : T/L/A/E Za.Zb.L.M.S.SA.	Usually terrestrial by river (ZP), semi-aquatic between rocks, lower parts submerged in wet season; in slow moving water, not in rocky rapids; occasionally epiphytic on riverside tree ferns (<i>Cyathea</i> , ZP).
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VII : as above
ZP, ZT, ZD = 1 sp.

<i>Cyclosorus interruptus</i>	a : T/A Za.Zb.B.M.N.SA.	Creeping terrestrial; underwater in wet season; riverside swamp (ZP), marshy stream on lower slopes (ZT), silted streamside (ZD).
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VII : as above
ZP, ZS, = 5 spp.

<i>Cyathea thomsonii</i>	o : T Za.Zb.M.	Tree fern; terrestrial, usually in shade at water's edge.
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<i>Pneumatopteris unita</i>	r : T Za.Zb.M.SA.	Terrestrial; on extreme edge of riverbank, extending over the water.
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<i>Diplazium zanzibaricum</i>	r : T/A Za.Zb.M.SA.	Terrestrial, like a small tree fern; in deep shade by river (ZP); by stream between conifer plantation on mountain slopes, just in water in wet season.
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<i>Marattia fraxinea</i>	a : T/A Za.Zb.M.SA.	Terrestrial, extremely large, spreading; almost in water at riverside, usually never more than 5m from water's edge.
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<i>Thelypteris confluens</i>	o to a : T/A Za.Zb.B.L.M.N.S.S.A.	Terrestrial to semi-aquatic; in river source (Mulunguzi Marsh), edges of Dams (ZP); at riverside (ZS), swampy in wet season. In slight shade or exposed positions.
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VII : as above
ZP, ZT = 1 sp

<i>Amauropelta bergiana</i>	r : T Za.Zb.M.S.S.A.	Terrestrial at riverside (ZP), by stream (ZT)
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VII : as above
ZS, ZT, ZD = 2 spp

<i>Christella dentata</i>	f : T Za.Zb.B.M.S.A.	Terrestrial at streamside; in slight shade or sheltered positions.
<i>Pteris friesii</i>	o to f : T Za.Zb.M.S.A.	Terrestrial; in deep shade in riverine areas, at bases of rocks, at edge of old <i>Cupressus</i> plantation.

VII : as above
ZS, ZT, = 3 spp.

<i>Asplenium pumilum</i>	o : T Za.Zb.	Usually terrestrial, in deep shade; on moist earthbank, at riverside; by small stream; on stonework of river bridge, in moss layer.
<i>Microlepia spelunca</i>	r : T Za.Zb.B.M.N.S.A	Terrestrial; rocky area near river, in sheltered positions at base of large rock.
<i>Pellaea doniana</i>	f : T Za.Zb.M.	Terrestrial, in deep shade on riverside bank; occasionally in shelter of rocks on woodland slopes.

VIII : seasonal pools (ZD only)
ZD only = 2 spp.

* <i>Ceratopteris thalictroides</i>	s* Za.Zb.B.M.S.S.A.	10-8-71, Howard-Williams 229 (MAL*). "growing in mud . . . partly submerged"
* <i>Marsilea</i> sp.	s* Za.Zb.B.M.N.S.A.	3-2-55. Jackson 1453A (MAL*), "growing in water of rice gardens"

IX : seasonal flush (all areas = 7 spp.)
ZP only = 1 sp.

<i>Ophioglossum polyphyllum</i>	r : T Zb.B.M.N.S.A.	Terrestrial, on rocky outcrop; at margin of montane grassland and montane forest.
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IX : as above
ZT only = 2 spp.

<i>Actiniopteris radiata</i>	r : T Za.Zb.B.N.S.S.A.	Terrestrial; rocky area with slight shade.
<i>Isoetes abyssinica</i>	r : T/A	Terrestrial; on level top of rocky outcrop; in shallow soil; water-logged in wet season.

IX : as above
ZP, ZS, ZT, ZD = 1 sp.

<i>Ophioglossum gomezianum</i>	a : T Za.Zb.	Terrestrial; in shallow soil on slopes and tops of rocky out-crops; may be water-logged in wet season.
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IX : as above
ZS, ZT, ZD = 1 sp.

<i>Actinopteris dimorpha</i>	a : T Za.Zb.B.M.N.SA.	Terrestrial; in outcrop areas, at edges of big boulders and in rock crevices; on rocky slopes below flush areas and on rocky roadside banks.
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IX : as above
ZS, ZT = 2 spp.

<i>Ophioglossum costatum</i>	f : T/A Za.Zb.	Terrestrial; on flat top of rocky outcrop, in shallow soil layer; usually water-logged in wet season; with <i>Isoetes</i> sp.
<i>Selaginella njam-njamensis</i>	a : T/L Za.	Terrestrial; edges of flush area; in small pockets of soil on rocky outcrop, extending growth over surrounding bare rock surface.

X : marginal habitats (all areas = 14 spp. including 1 var.)
ZP only = 2 spp.

<i>Athyrium schimperi</i>	o : T Za.Zb.L.SA.	Terrestrial; edges of forest and grassland and at cliff-top, often large plants; occasionally at riverside similar; very small plants under rock ledges on montane grassland and on roadside banks (ZP).
<i>Cheilanthes inaequalis</i>	o : T Za.Zb.B.M.SA.	Terrestrial; forest margins and edges of conifer plantations; in partly shaded positions.

X : as above
ZS only = 1 sp.

<i>Christella chaseana</i>	r ? : T Za.Zb.N.SA.	Terrestrial; edges of <i>Pinus</i> plantation.
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X : as above
ZP, ZS, ZT, ZD = 2 spp.

<i>Nephrolepis undulata</i>	a : T Za.Zb.M.	Terrestrial; edges of forest and plantations (ZP, ZS); in grassy areas of open woodland (ZS, ZT, ZD).
<i>Ophioglossum reticulatum</i>	a : T Za.Zb.L.N.SA.	Terrestrial; widespreading by underground stolons; at edges of forest and conifer plantations (ZP, ZS), woodlands (ZS), and in gardens, on Golf Course and lawns of the Botanic Garden, (ZT).

X : as above
ZP, ZS, ZT (4 spp. including 1 var. of a sp. in Habitat I).

<i>Dryopteris athamantica</i>	f to r : T Za.Zb.L.M.S.SA.	Erect terrestrial; frequent at roadside on montane grassland; occasional at montane grassland/forest margins; rare on lower slopes.
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<i>D. inaequalis</i> var. <i>inaequalis</i> (see Habitat I for other var.)	a : T Za.Zb.L.M.SA.	Tufted terrestrial with spreading fronds; in moist shady margins of forest and plantations (ZP, ZS), woodlands (ZS), and between river and cultivated areas (ZS, ZT).
<i>Pteridium</i> <i>aquilinum</i> subsp. <i>aquilinum</i>	a to r : T Za.Zb.L.M.SA.	Terrestrial; abundant at montane forest/ grassland margins, along forest paths, in clearings and at plantation margins (ZP, ZS); in open woodlands (ZS); rarely below 1000m (ZT), at edges of cultivation.
<i>Selaginella</i> <i>abyssinica</i>	a : T Za.Zb.M.	Terrestrial; usually upright but sometimes pendant on vertical earthbanks; at woodland edges and plantation margins (ZP, ZS), roadside banks (ZS, ZT). In slight shade or open areas.

X : as above
ZP, ZS = 5 spp.

<i>Asplenium</i> <i>buettneri</i>	r : T Za.M.	Tufted terrestrial; in deep shade; thicket at edge of montane forest (ZP); edge of <i>Pinus</i> plantation (ZS).
<i>Cheilanthes</i> <i>multifida</i>	a : T/L Za.Zb.L.M.N.SA.	Erect terrestrial; in most exposed margins of Plateau, edges of forest, plantations, cliff-edges; lithophyte of montane grassland/forest margins (ZP, ZS).
<i>Hypolepis</i> <i>sparsisora</i>	f to a : T Zb.M.S.SA.	Erect but spreading terrestrial; in wet partially shaded marginal areas; edges of riverine forest, stream edges of <i>Pinus</i> plantations; similar habit to <i>Pteridium</i> and often mixed with it, but only in moist places.
<i>Pellaea</i> <i>quadripinnata</i>	a : T Zb.L.M.N.S.SA.	Large erect terrestrial; on rocky montane grassland edges, cliff-edges (ZP); conifer plantations margins (ZP, ZS). In open or slight shade.
<i>Pteris</i> <i>catoptera</i>	a to f : T Za.Zb.M.SA.	Terrestrial; spreading fronds, very variable size; large plants inside edges of plantations (ZP, ZS), small along margins.

XI : sheltered habitats (all areas = 11 spp. including 1 var. of a sp. in Habitat XII).
ZT only = 4 spp.

<i>Platyserium</i> <i>elephantotis</i>	r (s) : E Za.M.	Epiphyte, in crown-base of old <i>Jacaranda</i> tree; one location.
<i>Adiantum</i> <i>raddianum</i>	o : T Zb.M.SA.	Terrestrial; on rocky roadside banks and in water channels, in slightly shady positions.
<i>Aspidotis</i> <i>schimperii</i>	r (s) : T Za.Zb	Tufted terrestrial; at edge of brick-built roadside ditch; in shade of trees. First collection for Zomba: 5-2-85, Berrie 600 (MAL).
<i>Ophioglossum</i> <i>vulgatum</i>	f : T Za.Zb.SA.	Terrestrial, spreading by under-ground stolons; in shaded grassy area ("lawn").

XI : as above
ZP, ZS, ZT, ZD = 1 sp.

<i>Pellaea</i> <i>calomelanos</i> var. <i>swynnertoniana</i>	f : T Zb.M.	Erect, tufted, terrestrial; edges of rocky outcrops, in rock crevices; on rocky roadside banks; usually slightly sheltered by trees or shrubs.
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XI : as above
ZP, ZS, ZT = 2 spp.

<i>Adiantum philippense</i>	a to r : T Za.Zb.M.SA.	Pendant terrestrial; on vertical earthbanks of forest roads (ZP, ZS); on rocky roadsides and bridges (ZS, ZT); in roadside ditches (ZT); usually in slightly shaded places. Rare on Plateau, abundant on lower mountain slopes.
<i>A. poiretii</i> var. <i>poiretii</i>	o : T Za.Zb.B.L.S.SA.	Terrestrial, may be mixed with <i>A. philippense</i> , in similar habitats but usually more shaded positions.

XI : as above
ZP, ZS = 1 sp.

<i>Selaginella mittenii</i>	f : T Za.Zb.L.S.SA.	Creeping terrestrial; in sheltered rock crevices; in moist shade below overhanging rocks.
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XI : as above
ZS, ZT, ZD = 1 sp. (var. of this sp. in Habitat XII)

<i>Doryopteris concolor</i> var. <i>kirkii</i>	f : T Za.Zb.M.N.SA.	Erect, tufted terrestrial; in shallow soil of rocky places; rock crevices; on bases of trees; roadside banks; usually in slight shade.
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(see Habitat XII for other var.)

XI : as above
ZS, ZT = 2 spp.

<i>Adiantum incisum</i>	r : T Za.Zb.M.N.SA.	Tufted terrestrial; in rock crevices, at edge of woodland (ZS); between stones of roadside wall, in heavy shade of trees (ZT).
<i>Pyrrosia schimperiana</i>	a : E/L Za.Zb.M.SA.	Creeping epiphyte; on upper trunk and main branches 3-6m from ground, on all sides and surfaces, pendant or erect fronds; on trees of upper and lower mountain slopes and ZT; lithophyte of lower slopes and ZT. Most common epiphyte of drier places around Zomba Mt.

XII : exposed habitats (all areas = 8 spp. + 1 var. = 9 spp.)
ZP only = 1 sp.

* <i>Mohria lepigera</i>	s* s* s* Za.Zb.M.	Sept. 1859 Kirk (K*), "Dzomba, Zambesia 6-7000ft". 20-5-82, Salubeni 3238 (MAL*), "on rocks in montane grassland" 7-4-84, Brummitt 17130 (K, MAL*), "steep rocky slope"
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XII : as above
ZT only = 1 sp. (var. of this sp. also in Habitat XI).

<i>Doryopteris concolor</i> *var. <i>nicklesii</i>	s* Za.Zb.	25-3-50, Sturgeon F2 (MAL*), "fully exposed rocky area" (cf. var. <i>kirkii</i> in Habitat XI.)
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XII : as above
ZD only = 1 sp.

* <i>Pellaea longipilosa</i>	s* Za.Zb.	14-3-77, Brummitt 14865 (K, MAL*), "rocky outcrop 2K E. of Zomba"
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XII : as above

ZP, ZS, ZT = 2 spp.

<i>Pellaea dura</i>	f : T Za.Zb.SA.	Small tufted terrestrial; in bare rocky places, open woodland and roadside banks; very exposed, extremely dry positions.
<i>P. viridis</i>	f : T Za.Zb.L.M.N.SA.	Terrestrial, tufted but spreading fronds; on rocky slopes of open woodland, and roadside banks; sometimes mixed with <i>P. dura</i> but not often extremely exposed.

XII : as above

ZP, ZS, = 4 spp.

<i>Arthropteris orientalis</i>	r : T/L Za.Zb.M.	Creeping terrestrial; on rocky open slopes; on top of rocky outcrop, in moss/thin soil layer.
<i>Lycopodium cernuum</i>	r : T Za.Zb.M.SA.	Creeping and upright, spreading terrestrial; on steep earthbank at roadside; open grassy bank near Dam; sometimes in slight shade.
<i>L. clavatum</i>	a to r : T Za.Zb.L.M.SA.	Wide-creeping terrestrial; in wet to very dry places; open streamside edge of <i>Pinus</i> plantation, marshy source of river, dry edges of <i>Eucalyptus</i> plantation, dry rocky roadside bank; can occasionally dominate the ground flora, especially after tree-felling.
<i>Mohria caffrorum</i>	a : T/L Za.Zb.L.M.SA.	Erect tufted terrestrial; on very exposed cliff-top grassland (ZP) and cliff-edges (ZP), and vertical rocky roadside (ZS).

Local and Regional distribution

Local distribution of species is given (a = abundant, f = frequent, o = occasional; r = rare; and s = single collection) for each species in each Habitat area. Some taxa have not been seen during the present study 1980-86. These are marked with an asterisk and local distribution is not given. Previous collections of these species are listed with their location in herbaria, using standard abbreviations (Stafleu, *et al* 1981). An asterisk there, e.g. K*, indicates that particular specimen was seen by me at that herbarium in Sept. 1986.

Regional distribution of each species is given for the whole of Southern Africa, taken from the most recent available literature as follows, (abbreviations for each country in brackets): Zambia (Za) Kornaś 1979; Zimbabwe (Zb), Burrows 1983; and all others from Jacobsen 1983, Botswana (B), Lesotho (L), Mozambique (M), Namibia (N), Swaziland (S) and South Africa (SA).

Plant habit

The terms epiphyte (E), lithophyte (L), terrestrial (T), and aquatic (A), are used to describe plant habit, with further detailed descriptions of each species. Alternative habits showing the most usual habit as first letter, include E/L, E/T/L, T/E, T/L, T/A and T/L/A/E.

TABLE 2

Plant habit. Number of species of each plant habit type in Habitats I-XII. (Abbreviations: E = epiphytic, T = terrestrial, L = lithophytic, A = aquatic; with alternative habits the first letter indicates the most usual habit. An asterisk * marks a species or variety not seen in the present study, these are not included in the final % totals).

Habitat, and number of species in each	PLANT HABIT								L	A
	E	E/L	E/T/L	T/E	T/L	T/L/A/E	T/A	T		
I: 5 spp. (incl. 1 sp/v in Habitat X)	1			2				1 + 1 sp/v		
II: 3 spp.		2	1							
III: 5 spp.	4							1		
IV: 1 sp.								1		
V: 12 spp.	2 + 1*				1*			3 + 2*	3*	
VI 8 spp.	1	4	1	1				1		
VII: 20 spp.	1					1	5	12 + 1*		
VIII: 2 spp.										2*
IX: 7 spp.					1		2	4		
X: 14 spp. (13 + 1 sp/v in Habitat I)					1			12 + 1 sp/v		
XI: 11 spp. (incl. 1 sp/v in Habitat XII)	1	1						8 + 1 sp/v		
XII: 9 spp. (8 + 1 sp/v in Habitat XI)					2 + 1*			4	1* + 1 sp/v*	
total 95 spp. 83 + 12 spp.* (+ 1 sp/v*)	= 10 = 1*	+7	+2	+3	+4 +2*	+1	+7	+49 +3*	0 +4spp* & 1sp/v*	0 +2spp*
% of total:	10.5 E = 20% (+1%*)	7.4	2.1	3.2	4.2	1	7.4	51.6	0 L = 0 (+4.2%*)	0 A = 0 (+2.1%*)

In some rocky habitats it is difficult to distinguish between terrestrial and lithophytic habit but any plant rooted in soil of more than 1cm depth is listed as T. The lithophytes may be in a moss layer on rock or very shallow soil layer, but they are never on a completely bare rock surface.

ECOLOGY

Montane forest pteridophytes occur in Habitats I, II, III, and VI showing that there are

a number of microhabitats or niches within montane forest in which groups of pteridophyte species are found together (Figure 6).

Habitat I includes the darkest, wettest part of montane forest and only five species are here. There is very little ground flora other than scattered ferns. *Dryopteris inaequalis* var. *atropaleacea* is in very deep shade near the edge of the forest, inside the thicket of *Philippia* and *Hypericum*. The contrast in light intensity from the open grassland outside the forest into this thicket is extreme. Similarly in the deepest part of the forest, near the small stream, it is dark due to the dense canopy of the continuous tree-cover. The other four species are in this darkest part, *Asplenium lobatum* in one small dark area of ground, with *A. boltonii* and *A. dregeanum* either terrestrial or very low level epiphytes on tree bases and rotting tree stumps. *Elaphoglossum acrostichoides* is also only in one site, like *A. lobatum*, in the darkest part. It is an epiphyte on a small tree with an extremely thick canopy. All these species are well away from the more open pathways going through the forest.

Habitat II and III include those parts where just a little bit more light penetrates the forest, whether in montane, riverine or cliff-edge forest. In the montane forest where the canopy is somewhat open because of fallen tree branches, or near pathways where tree saplings have been cut to keep the path open, there are many fern species which also occur in riverine forest since the microhabitat is similar. Much of the montane forest is like this, with deep moist leaf litter and permanently wet soil. The air is moist at all times and epiphytic ferns are most luxuriant. The filmy ferns cover tree bases and tree trunks up to 2 or 3cm from the ground with *Asplenium mannii* and *A. sandersonii* occurring with them at 1-1.5m. The maximum number and abundance of species occurs at about 2-3m level where the whole surface of tree trunks is wet and dripping and covered with ferns.

Above this level the epiphytes are more spread out on the branches, these are the species included in Habitat VI. The conditions on the mid to upper parts of the tree crowns of the montane forest are very similar to those found on trunks and crown bases in riverine and remnant riverine forest at lower altitudes on the mountain; they are also similar to some parts of the closed woodland on the mountain slopes, so the eight species in Habitat VI list are the most widespread of the forest/woodland pteridophyte species. In different locations some of these ferns occupy similar niches e.g. *Pleopeltis excavata*, *P. macrocarpa*, *Loxogramme lanceolata* and *Pyrrosia rhodesiana* are all epiphytes in montane and riverine forest, but at lower altitudes (ZS) may be lithophytes in remnant riverine forest. The position of the epiphytes on the trees depends on the amount of light penetrating the canopy and the available water, either run-off with most at the tree base or high humidity and condensation in the crown-base. The filmy ferns thrive in the optimum conditions of the montane forest, but only survive in a few places of the riverine forest and cliff-edge forest thicket, and are completely absent from remnant riverine forest (ZP, ZS) and the woodlands (ZS).

Similarly in riverine forest only (Habitat V), there are some species e.g. *Selaginella kraussiana* and *Blechnum attenuatum*, which thrive in the continuously moist habitat but require some tree-cover. They can withstand some shading but not continuous exposure. One small part of the riverine forest where *Blotiella natalensis* occurs has a very dense ground flora of *S. kraussiana*, and a nearby large tree (*Rauvolfia* sp.) has a complete covering of filmy ferns from ground level to 2m, together with *Asplenium mannii*, *A. sandersonii* and *L. lanceolata*, and looks very like the tree bases in the montane forest. But here the riverine forest canopy is higher and more light penetrates, although there is deep shade in some parts, so *S. kraussiana* flourishes because of the very wet soil conditions. Around the plants of *B. natalensis* the water table is almost at the surface in the dry seasons and some of that area is flooded during the wet season.

Six of the species listed in Habitat V, riverine forest only, have not been seen recently (1980-86) and may no longer be present on Zomba Mt. The felling of *Pinus patula* on some of the sloping ground near the river has sometimes severely damaged trees closer

to the river, so these have had to be felled also. In some places along the river there has been very little regeneration of the riverine forest due to the slashing (cutting back of ground flora) to keep riverside paths clear for the tourists and trout-fishermen. This means that when old trees, e.g. of *Halleria lucida*, lose branches, fall to pieces gradually, and eventually rot away then the particular epiphytes on that tree may be lost, perhaps permanently from that area. The tree gap opens up the canopy and if no young saplings take the place of the old tree then what was riverine forest becomes more open remnant forest, in which some of the terrestrial or lithophytic ferns also cannot survive. Certainly this has happened with *Polypodium polypodioides*, an epiphytic fern, frequent to occasional in distribution in 1967. There are now very few trees with long, low overhanging branches stretching out over the water as there were then, in that part of the Mulunguzi River just below the Trout Ponds. The river is wider now from erosion, the undermining of the riverbank is partly due to slashing very close to the edge so that young ferns (*Cyathea* spp. and *Marattia*) are not able to get established easily by the water.

Much of the riverside vegetation between the plantations is no longer forest or even remnant forest. It is just a very wet habitat, sometimes partly shaded by nearby trees in the *Pinus* plantations, so the pteridophytes along the river and streams have been listed in Habitat VII. These species are often standing in water during the wet season. They may be exposed to full sunshine, though proximity to open water usually gives a high air humidity. Where there was forest or remnant forest twenty years ago there is now in some parts just a line of tree ferns. *Cyathea dregei* is the most abundant and is rarely far from the water's edge. *C. thomsonii* is more scattered along the river, growing with *C. dregei*. *Marattia fraxinea* is the most conspicuous of the large ferns, usually rooted only a few metres from the water, with fronds 3-4m long spreading out almost into the conifer plantations alongside. *Marattia* is usually on the silted side of the river while the opposite banks have masses of *Osmunda regalis*, rooted between large rocks where little silting has occurred. All these species are in shallow water where the river is slow moving. None are found where the river is narrow and rapid flowing. The bed of the river changes greatly within short distances, from rapids to meanders, to waterfalls and narrow mini-gorges between large boulders, and back to wider meanders with small sandy patches on one side.

The pteridophyte species distribution reflects these changes in different parts of the Mulunguzi River from the narrow source below Mulunguzi Marsh, downstream as far as Mulunguzi Dam. Below the Dam there is remnant riverine forest in parts, almost to the top of the Gorge. Here the river goes over a high waterfall through narrow cliffs. Below the falls there is more open rocky banks with scattered trees along the river. In the spray of the falls is a single location for *Vittaria volkensii*, a mid-level epiphyte, and close-by among rocks a few plants of *Cheilanthes farinosa*. Ten to 15m from the river, as by small streams on the lower slopes, are scattered small plants of *Asplenium pumilum*, and the rarer but larger *Microlepia speluncae*. Both are short-lived, not surviving long after the rains stop, because at this altitude (c.1100m), away from the tree cover, dry conditions soon take over.

Away from the river and streams, at edges of forest/woodland or forest/grassland are some pteridophyte species with a wide distribution on many parts of the mountain. These are marginal habitat species (Habitat X). The most prominent is *Pteridium aquilinum* (bracken), which can survive and spread even in poor rocky soil. In many parts of the Plateau it is dormant in the *Pinus* plantations. In years 1-3 after planting *Pinus* seedlings, bracken is cut between the young trees but after that does not grow up again due to heavy shading. It remains along pathways and edges of plantations, but at clear-felling 25-30 years later it sprouts up again all over the newly felled area. *Pteris catoptera* also has a tendency to re-appear further into the felled conifer areas, but may be re-colonising rather than remaining dormant in the soil like the *Pteridium*.

In wet marginal areas *Pteridium* is often mixed with *Hypolepis sparsisora*. With similar growth habit they can be confused from a distance but the delicate paler green of the *Hypolepis* can be picked out in the wetter parts of this habitat on the Plateau and the slopes. At lower altitudes, ZT and ZD, *Nephrolepis undulata* is the most widespread marginal species in grassy/woodland areas while at higher latitudes along cliff-edges are *Pellaea quadripinnata*, *Cheilanthes multifida* and *C. inaequalis*. All these species in marginal habitats get some shelter from nearby trees, but can be exposed to very dry conditions at some time of year. Most die back during the dry season to some extent on the Plateau, some die back completely at lower levels, but by looking for more sheltered "favourable" marginal habitats it is usually possible to find some plants of these species at almost any time of year on some part of the mountain.

The remaining habitats (VIII: seasonal pools, IX: seasonal flush, XI: sheltered, and XII: exposed) have much more extreme conditions from wet to dry seasons. There are no seasonal pools on Zomba Mt. but in low lying parts of Zomba District some water ferns may be found. Two genera (*Ceratopteris* and *Marsilea*) have been recorded, though I have not seen any recently, 1980-86, in the Zomba area*. Seasonal flush habitats are more common around the lower slopes of Zomba Mt. where rocky outcrops are found. These areas have smooth, rounded, granite domes with flattened tops, or small flat ledges on some part of the slope. Small pockets of soil on the rock quickly become soaked in the first rain of the season and then water-logged as seepage continues from deeper soil higher up the slope. The whole rock surface may then have a thin water flow over it for many weeks of the wet season. A short dry spell with no rain, e.g. 2 or 3 weeks in early December, can cause complete drying out and curling up of the soil pocket, so conditions can be extreme even during the wet season.

In such places *Ophioglossum* spp. appear each year. *O. costatum* is first with the early flowering monocots (*Platycorine*, *Dipcadi* and *Lapeirousia* spp.) in the wettest parts low on the outcrop. Higher up the granite slope and on the flat top with deeper peaty soil come later species, *O. gomezianum* being abundant and widely distributed, and *O. polyphyllum* much rarer only in one location. In the wettest parts the later (Jan-Feb.) arrival of *Isoetes* sp. completes the *O. costatum* community. Another outcrop area, not so wet, has *Isoetes* with *O. gomezianum* and patches of *Selaginella njam-njamensis*. At the edges of seasonal flush areas clumps of *Actiniopteris* spp. occur.

The seasonal flush habitat grades into the sheltered (XI) and the exposed (XII) habitats particularly on poorer stony soil. The terrestrial ferns *Adiantum* spp., *Pellaea* spp., *Doryopteris concolor* and *Mohria* spp. are all in these very dry habitats with varying amounts of shade or exposure. The only epiphyte which is abundant in drier places is *Pyrrosia schimperiana*.

The only fern found recently in Zomba and not listed in Table 1 in Habitats I-XII is one which appeared amongst other ferns in trays in the greenhouse. Some samples of *Ophioglossum reticulatum* were collected with a large amount of soil on 23-3-84 from margins of a *Pinus patula* plantation on Naisi Spur (ZS). They were planted in that soil in trays in the Biology Dept. greenhouse at Chancellor College, Zomba (ZD). Sometime later, in June, small sporelings of *Pityrogramma calomelanos* (L.) Link var. *calomelanos* appeared in the tray with the *Ophioglossum*. *P. calomelanos* is not previously recorded for Zomba and I have not found it in the wild, nor seen it in cultivation here. The specimen in MAL. is Berrie 422B, 7-6-84, 'weed in tray of *Ophioglossum reticulatum* in Biology Dept. greenhouse, CC.' It is only included here to complete the listing of all known pteridophytes from the Zomba area, thus the total pteridophyte taxa for Zomba, including this weed species, are 96 species in 46 genera of 22 families, but *P. calomelanos* is not included in Table 1.

*My collection closest to Zomba is *M. subterranea* Lepr. from Mangochi District, 100km north of Zomba, Berrie 316 (BM, MAL), 8-4-82; the most southern record for this species (Launert, pers. comm. 1984).

DISCUSSION

The 95 species listed in Table 1 include 45 genera in 22 families of pteridophytes. This is a relatively high number for Africa since a total of 55 species is the estimate for the whole of tropical Africa (Parris 1985). Thus Zomba Mt. has 19% of this total in an area of approx. 8 x 12km. This compares with the Zambia records (Kornaś 1979) where the highest number of pteridophyte species in a one degree square (1°lat x 1°long., approximately 100km x 100km) is 56 species or 11% of the total for Africa. The Lusaka District at approximately the same latitude as Zomba, but 800km due west at longitude 28-29°E, has 31 species, only 6.2%. Lusaka, the Zambian capital, at 1278m altitude has only 835mm mean annual rainfall compared to Zomba (alt. 900m) with 1464mm, and Zomba Plateau (alt. 1900m) with 2244mm mean annual rainfall. This big difference in rainfall is probably the main cause of the big difference in number of pteridophyte species between Lusaka and Zomba.

Similarly on Zomba Mt. the differences between the Plateau rainfall and the Town rainfall is reflected in the plant distribution and particularly in the distribution of the pteridophyte species. The montane forest is only on Zomba Plateau and most of the riverine forest is also on the Plateau. The pteridophyte numbers in these forests are 21 spp. in montane and 29 spp. in riverine, with 16 spp. common to both (Figure 6b). Of the 68 spp. in all habitats (Fig. 6e) on Zomba Plateau there are 32 forest/woodland species with 22 of these restricted to ZP. (Fig. 6a & b). The number of forest/woodland species, like the rainfall, decreases with altitude from ZP, 32; ZS, 10; ZT, 5 and ZD, 2 spp. The marginal habitat species follow the same pattern with ZP, 13; ZS, 12; ZT, 6 and ZD, 2 spp. The riverside non-forest (VII) habitat has a slightly different pattern with ZP, 11; ZS, 16; ZT, 10 and ZD, 4 spp. and has discontinuous distribution (3 spp.) also, not found in the other habitats. This reflects the particular microhabitat required by these three species rather than being related to altitude or rainfall. This is shown by *Osmunda regalis* on ZP, ZS and in ZD. The Mulunguzi River in ZT has rapid flowing water, mostly a narrow riverbed with huge rocks and boulders at each side. *Osmunda* grows on sandy, silted banks or between small rocks in slower water so it is not found in ZT. *Osmunda* is also only by the main river, not by small streams which dry out completely in the dry season. *Cyclosorus interruptus* is similar with swampy riverine area (ZP), muddy streamside (ZT) and silted, swampy stream (ZD) being the microhabitats in three areas, but no suitable places occur on ZS for it. *Amauropelta bergiana* (ZP and ZT) may be undercollected, since the genera of Thelypteridaceae, being very alike, need further investigation ecologically. *Christella chaseana* (Habitat X: marginal, ZS) in the same family is also queried (?r) in distribution, needing further collection.

The flush habitat (IX) and sheltered habitat (XI) have similar patterns with more species on the mid-mountain slopes and township area (ZS, ZT), while the exposed habitat (XIII) reverts to the pattern of Habitats I-VI. Taking these all together (Fig. 6e) gives a clear picture of greater numbers of species at higher altitudes, ZP 68 spp. (72% of total spp.), ZS 55 spp. (58%), ZT 39 spp. (41%) and ZD 15 spp. (16%). The factors affecting this distribution due to altitude are the increased rainfall at higher altitudes; greater tree-cover i.e. thicker forest on the higher land; riverine and remnant riverine on ZP and ZS; woodland on upper and lower slopes; and the amount of condensation-cloud on the Plateau and upper slopes especially during the dry season. The higher temperature at lower altitudes, with the very strong dry winds of mid-dry season (Aug.), will also combine with the lack of tree-cover, in ZD, to give a smaller number of species. Only in streamside habitat can they survive the dry season, if the stream is a permanent one.

An analysis of the plant habit of species in the different habitats (Table 2) shows 20% of the 95 species are usually epiphytic though 9.5% may occasionally be lithophytic or terrestrial. 51.6% of the total are always terrestrial while 7 spp. (7.4%) are so close to

water as to be sometimes actually in it, classed as T/A. Only 2 spp. (2.1%) are true aquatic ferns.

Habitat V (riverine forest only) has suffered the most since the 1960's if the species marked are not any longer present on Zomba Mt. These species are 3 lithophytic, 2 terrestrial, 1 T/L, and 1 epiphyte all previously recorded from riverine areas. During the 1980-86 period I have made observations on the pteridophyte flora of most parts of Zomba Mt. I know all these species from other parts of Malawi and it is possible they may be on the mountain, in some place where I have not seen them, if so I would regard them as threatened species.

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PRELIMINARY REPORT OF CHROMOSOME COUNTS IN THE GENUS *AZOLLA* (PTERIDOPHYTA)

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ABSTRACT

Contrary to previous reports, study of chromosome numbers in the genus *Azolla* establishes the occurrence of $2n=44$ in all species except *A. nilotica* which has $2n=52$. In addition, triploid clones ($2n=66$) were found in some species and a single tetraploid clone of *A. pinnata* ($2n=88$) is recorded for the first time in the genus.

INTRODUCTION

Azolla Lam. is a genus of heterosporous aquatic ferns with a world-wide distribution in tropical to temperate regions. Five species are currently recognised within section *Azolla*: *A. filiculoides* Lam., *A. rubra* R.Br., *A. caroliniana* Willd., *A. mexicana* Presl and *A. microphylla* Kaulf.; and two species in section *Rhizosperma* (Mey.) Mett.: *A. nilotica* Decne. ex Mett. and *A. pinnata* R. Br. Chromosome numbers are recorded for most species but show contradictory results, and are often based on a single clone (Litardi re 1921, Tschermak-Woess & Dolezal-Janisch 1959, Loyal 1958, Loyal, Gollen & Ratra 1982, Thanh 1983, Singh, Patra & Nayak 1984, Lin & Sleep 1988).

MATERIALS AND METHODS

Extensive investigation of somatic chromosome numbers in *Azolla* is in progress at Portsmouth Polytechnic. Approximately eighty clones of all species from widely separate regions within the geographical range of the genus have been studied (Table 1). It should be mentioned, however, that only two clones of *A. nilotica* were obtained, and more material will need to be examined. The large number and small size of chromosomes in *Azolla* indicate that meiotic rather than somatic material would be easier to examine. Vegetative material was used, however, because it is generally considered more appropriate in establishing reliable chromosome numbers in unknown taxa. Shoot tips were pretreated in 0.1% colchicine for 5 hours and transferred to 3:1 absolute alcohol: glacial acetic acid for at least 24 hours. The material was then hydrolysed in 1 M HCl at 60 C for 7 mins., stained with Feulgen for 1 hour and squashed in acetocarmine. Voucher herbarium specimens will be deposited at the British Museum (Natural History).

TABLE 1

Number of clones of species studied and their distribution range.

Species	Clones	Geographical distribution (* species introduced)
<i>A. filiculoides</i>	13	Europe *; North, Central & South America; East Asia *.
<i>A. rubra</i>	2	Australasia.
<i>A. caroliniana</i>	16	Europe *; Central Africa *; North, Central & South America.
<i>A. mexicana</i>	9	North & South America; East Asia *.
<i>A. microphylla</i>	13	Central & South America.
<i>A. nilotica</i>	2	East Africa.
<i>A. pinnata</i>	26	West, East, Central & South Africa; India; Southeast Asia; East Asia; Australasia.

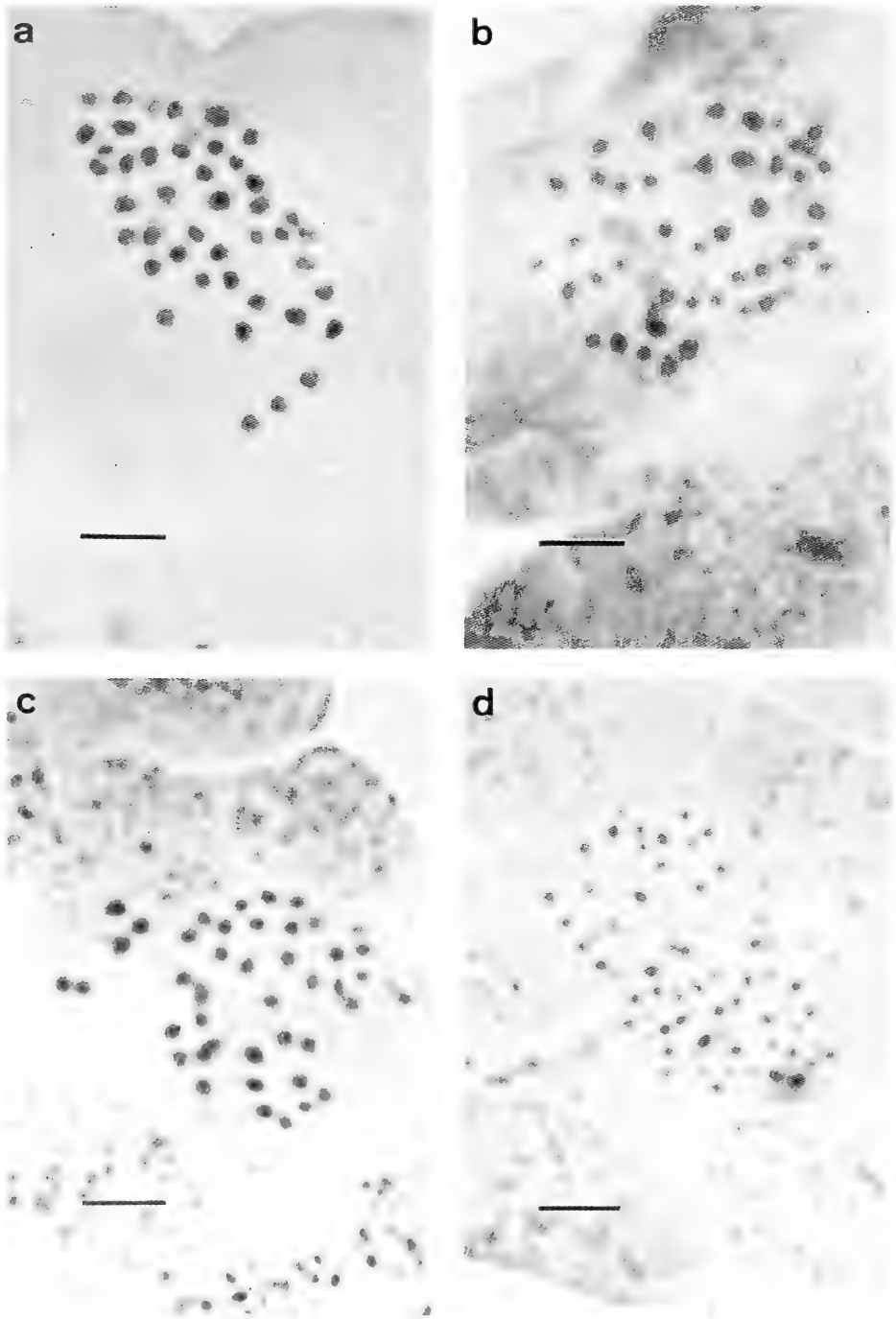


FIGURE 1. Mitotic metaphases (Scale bar = 3 μ m).

a) *A. filiculoides* showing $2n=44$. (Portsmouth Polytechnic Coll. No. 103, UK)

b) *A. caroliniana* showing $2n=44$. (IRRI Coll. No. 3002, USA)

c) *A. microphylla* showing $2n=44$. (IRRI Coll. No. 4018, Paraguay)

d) Triploid *A. pinnata* showing $2n=66$. (IRRI Coll. No. 5, Thailand)

RESULTS AND DISCUSSION

Despite previous reports to the contrary, the results indicate that the chromosome number is invariable and will provide little information useful for taxonomic separation, particularly in section *Azolla*. With the exception of *A. nilotica*, which was found to be $2n=52$, counts of $2n=44$ were recorded from clones of all the other species (Fig. 1a, b and c). Most species in section *Azolla* appear to have similar chromosome size. Although *A. pinnata* (section *Rhizosperma*) has the same chromosome number as species of section *Azolla*, it has distinctly smaller chromosomes. Triploid counts ($2n=66$) were recorded in both sections of the genus. In section *Azolla*, triploidy was found in only one clone of *A. filiculoides* (from Bolivia) and *A. microphylla* (from Mexico), and in two clones of *A. caroliniana* (from Brazil and Mexico). In section *Rhizosperma* triploids appear to be more frequent, being found in five clones of *A. pinnata* from Nigeria, Sri Lanka, Thailand, China and Australia (Fig. 1d). The incidence of tetraploidy ($2n=88$) was low, being found in only a single clone of *A. pinnata* from Bangkok. Further investigations aim to clarify whether the triploid clones have resulted from hybridisation between tetraploid and diploid clones, or are produced by the occasional function of unreduced gametes. Functional unreduced gametes are usually derived from interspecific hybrids, but can also be produced from species clones under certain environmental conditions. Further meiotic or electrophoretic studies of these triploids may establish whether they are auto- or allotriploids, and could provide evidence for their origin. It remains to be discovered whether the clone of *A. pinnata* represents a tetraploid population or is simply a unique clone, and if tetraploid populations occur.

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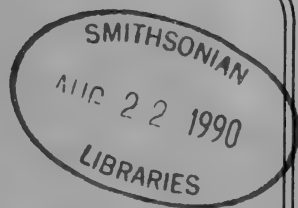
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SCANNING ELECTRON MICROSCOPE PHOTOGRAPHS OF THE SORI AND SPORES OF SIX SPECIES OF RUST FUNGI (UREDINALES) FOUND ON FERNS IN BRITAIN

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ABSTRACT

Scanning electron microscope photographs are presented of *Dryopteris dilatata* and *Abies alba* with the rust *Milesina kriegiana*; *Blechnum spicant* and *Abies alba* with *Milesina blechni*; *Asplenium scolopendrium* and *Abies alba* with *Milesina scolopendrii*; *Polypodium interjectum* with *Milesina dieteliana*; *Phegopteris connectilis* with *Uredinopsis filicina*; and *Cystopteris fragilis* with *Hyalopsora polypodii*. In each case a sorus of the rust and individual spores at high magnification are shown. A table is included of other British ferns on which rust fungi have been recorded. The need for more information about the occurrence and distribution of these rusts on ferns in Britain is emphasised.

INTRODUCTION

A review of the literature in relation to an introductory S.E.M. atlas of sori and spores of some rusts (Preece and Hick 1989) and many discussions with other biologists in relation to rust fungi clearly indicated two things in relation to rusts on ferns. No British plant pathologist we discussed the matter with was aware that there **were** rusts on ferns, and eminent pteridologists were equally uncertain as to whether they occurred, or not! A thorough review of the literature and discussion of the fern rusts is long overdue.

This is **not** such a review, but a presentation of S.E.M. photographs of six fern rusts collected in Britain, and of which no S.E.M. photographs exist in the literature.

Rust workers have thought rusts on ferns to be the primitive forms from which other rusts, (on angiosperms), have evolved (Ando 1984). An important recent cladistic analysis suggests however that this is not the case, and that tropical short-cycled rusts (usually with only urediniospores) are the basal group in the evolution of rust fungi (Hart 1988). We do not ascribe any specific biological usefulness, hypothesize about phylogenetic connections, or speculate about the beautiful surface ornamentation visible in the S.E.M. pictures presented in this brief paper. We hope that these pictures will encourage others to consider these matters. It might be that (as with other rust fungi on other plants) the extreme host specificity of the rusts is of taxonomic value to pteridologists? At the very least we hope to encourage British fern-workers to look out for rusts and thus enable our knowledge of the occurrence and distribution of rust fungi on ferns in the British Isles to expand. We would welcome specimens from any location, pressed and dry (**not** in plastic bags).

According to Peterson (1974) the general rust fungus life cycle is the "most plastic and complex" series of events known for any kind of living organism. Only the life cycles of certain animal parasites approach the complexity of those of rust fungi on plants, and quite an effort is necessary to grasp both the sequence of events in the life cycle of any rust fungus, the function of the various stages in the life cycle, and the different spores of each species which occur. An explanatory outline of these matters of rust form and function is given in Preece & Hick (1989), together with references enabling the reader to find light microscope drawings of most of the rusts on plants (including ferns) found in Britain.

All the five types of rust spores: *teliospores* borne on telia; *basidiospores* produced from the basidia on teliospores; *spermatia* borne on spermatogonia; *aeciospores* borne in aecia and *urediniospores* borne on uredinia, may be produced on the same plant host, or on two plant hosts. In the latter case, the urediniospores and teliospores are usually found on one host and the spermatia, with the aeciospores, on the other host. Some spore types may be missing from particular rusts. These missing stages either do not exist, or

have not yet been found. Where an alternate host is known for any British fern rust, it is a gymnosperm – a conifer, of the genus *Abies*. The teliospores of fern rusts, where they are known, are enclosed *within* the epidermis and in some cases the leaf mesophyll cells and cannot be illustrated by scanning electron microscopy. More microscopic studies of the production of basidiospores from the teliospores of fern rusts are needed, and also of the spermatia which precede the production of aecia on fir needles.

There are very few scanning electron microscope pictures of fern rust sori or spores in the literature. Littlefield & Heath (1979) included S.E.M. pictures of the urediniospores of *Uredinopsis osmundae* (which occurs in the USA on *Osmunda* spp.) showing their smooth surfaces with an erect wall-like irregular thickened ridge running along opposite sides of the spore, and also S.E.M. pictures of urediniospores of *Milesia laeviuscula* (which according to Arthur 1934 occurs in the U.S.A. on *Polypodium californicum* and *P. glycyrrhiza*) which are completely smooth. Littlefield & Heath used their pictures to illustrate the range of surface ornamentation (or lack of it) on the urediniospores of rusts in general.

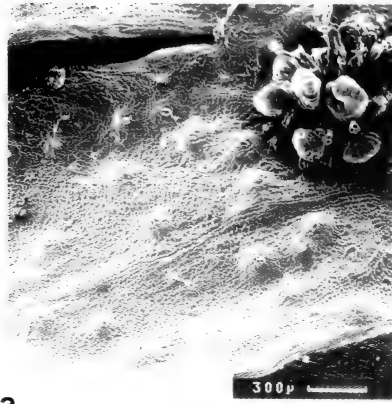
Using S.E.M., Hafellner & Grill (1982) have shown that the urediniospores of *Milesia vogesiaca* on *Polystichum aculeatum* and *P. lonchitis* are not smooth, as was thought to be the case by light microscopy, but finely verrucose. These authors confirmed, however, that the urediniospores of the rust *Milesia whitei* on *P. aculeatum* were typically echinulate.

TABLE I

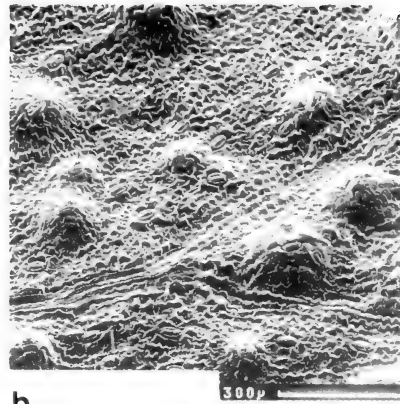
List of British ferns, by Family, and the species of rust fungi so far recorded on them*

OPHIOGLOSSACEAE	No rusts recorded in Britain
OSMUNDACEAE	No rusts recorded in Britain
ADIANTACEAE	
<i>Adiantum capillus-veneris</i> :	<i>Hyalopsora adianti-capilli-veneris</i>
HYMENOPHYLLACEAE	No rusts recorded in Britain
POLYPODIACEAE	
<i>Polypodium vulgare (sensu lato)</i> :	<i>Milesina dieteliana</i>
HYPOLEPIDACEAE	No rusts recorded in Britain
THELYPTERIDACEAE	
<i>Phegopteris connectilis</i> :	<i>Uredinopsis filicina</i>
ASPLENIACEAE	
<i>Asplenium scolopendrium</i> :	<i>Milesina scolopendrii</i>
<i>A. adiantum-nigrum</i> :	<i>Milesina magnusiana</i>
<i>A. ruta-muraria</i> :	<i>Milesina murariae</i>
ATHYRIACEAE	
<i>Gymnocarpium dryopteris</i> :	<i>Hyalopsora aspidiotus</i>
<i>Cystopteris fragilis</i> :	<i>Hyalopsora polypodii</i>
ASPIDACEAE	
<i>Polystichum aculeatum</i> :	<i>Milesina vogesiaca</i>
<i>Polystichum setiferum</i> :	<i>Milesina whitei</i>
	<i>Milesina vogesiaca</i>
<i>Dryopteris filix-mas</i> :	<i>Milesina carpatorum</i>
	<i>Milesina kriegneriana</i>
<i>Dryopteris affinis (sensu lato)</i> :	<i>Milesina kriegneriana</i>
<i>Dryopteris carthusiana</i> :	<i>Milesina kriegneriana</i>
BLECHNACEAE	
<i>Blechnum spicant</i> :	<i>Milesina blechni</i>

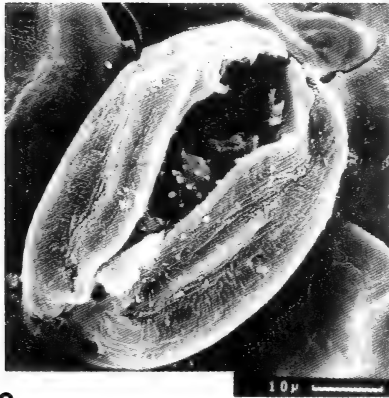
* Fern family and species nomenclature from Clapham, Tutin & Moore (1988). Fern rusts according to Wilson & Henderson (1966) and Ellis & Ellis (1985)



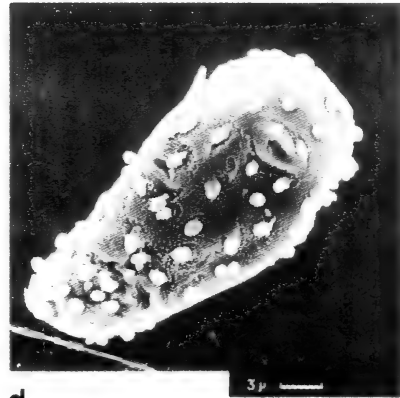
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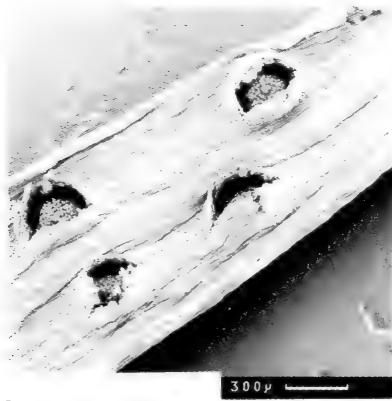
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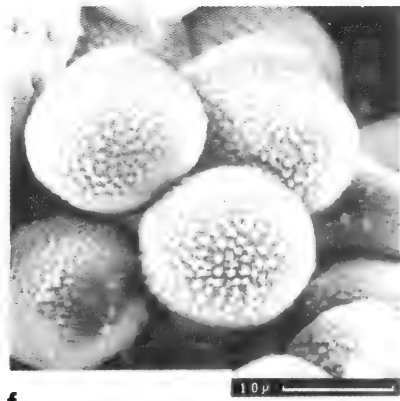
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FIGURE 1: *Dryopteris dilatata* with the rust *Milesina kriegneriana*: a) fern sporangia and rust sori to show relative sizes on frond on brown necrotic area; b) rust sori at higher magnification; c) rust urediniospore seen below stoma; d) single rust urediniospore. *Abies alba* with the rust *Milesina kriegneriana*: e) accia on lower surface of needle; f) acciospores from accium.

Using carbon replicas, Henderson & Prentice (1977) showed the echinulations on the urediniospores of *Milesina blechni* on *Blechnum spicant* to develop in the same way as those of the urediniospores of other rust fungi. Spines arise within the primary urediniospore wall, followed by the deposition within it of a thicker secondary wall. This secondary spore wall becomes the spore wall normally seen, with the spines exposed by loss of the primary wall. A list of the ferns occurring in the British Isles according to Clapham, Tutin & Moore (1988) is given in Table 1, together with the names of the rusts which occur on fifteen of these fern species. Out of eleven families of ferns, four: the Ophioglossaceae, Osmundaceae, Hymenophyllaceae and Hypolepidaceae have no rusts recorded on them in Britain. Four ferns, *Dryopteris filix-mas*, *D. affinis* (*sensu lato*), *D. carthusiana* and *D. dilatata*, have the same rust (*Milesina kriegeriana*) on them. Two ferns, *Polystichum aculeatum* and *Polystichum setiferum*, have the same rust recorded on them (*Milesina vogesiaca*). Two ferns have two rusts on each species (*Polystichum setiferum* with *Milesina whitei* and *M. vogesiaca*; *Dryopteris filix-mas* with *Milesina carpatorum* and *M. kriegeriana*). Almost all the Figures in this paper are of Yorkshire fern rust specimens, and the material was prepared from herbarium specimens (some very old) as described in Preece & Hick (1989).

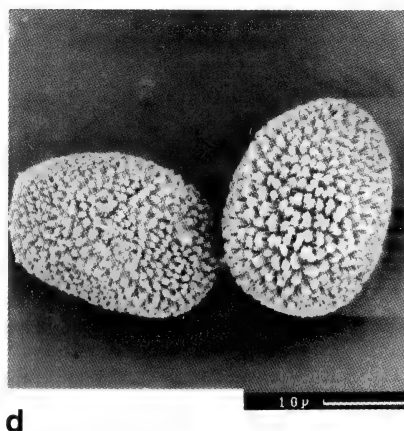
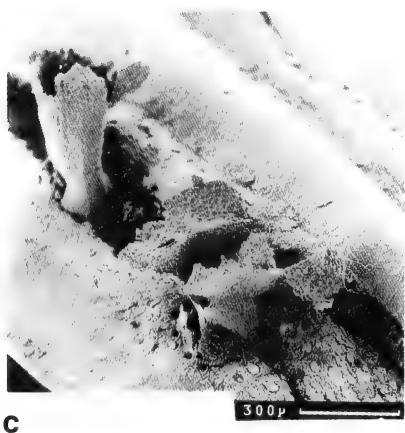
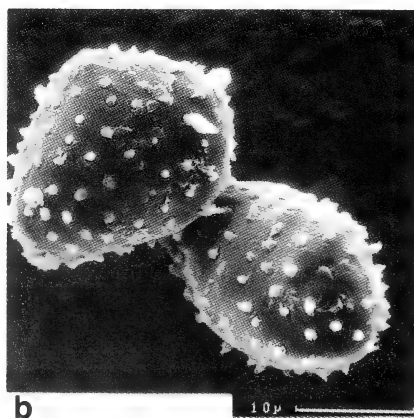
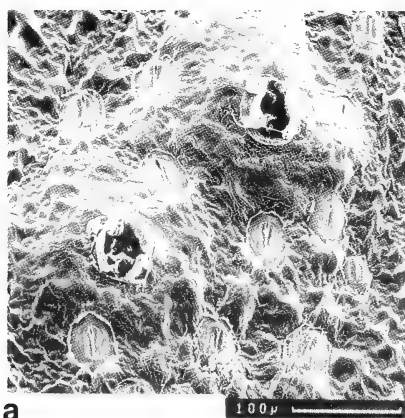


FIGURE 2: *Blechnum spicant* with the rust *Milesina blechni*: a) portion of fern frond with two rust sori on brown area; b) two urediniospores from sorus. *Abies alba* with the rust *Milesina blechni*: c) lower surface of needle with acia; d) aeciospores from aecium.

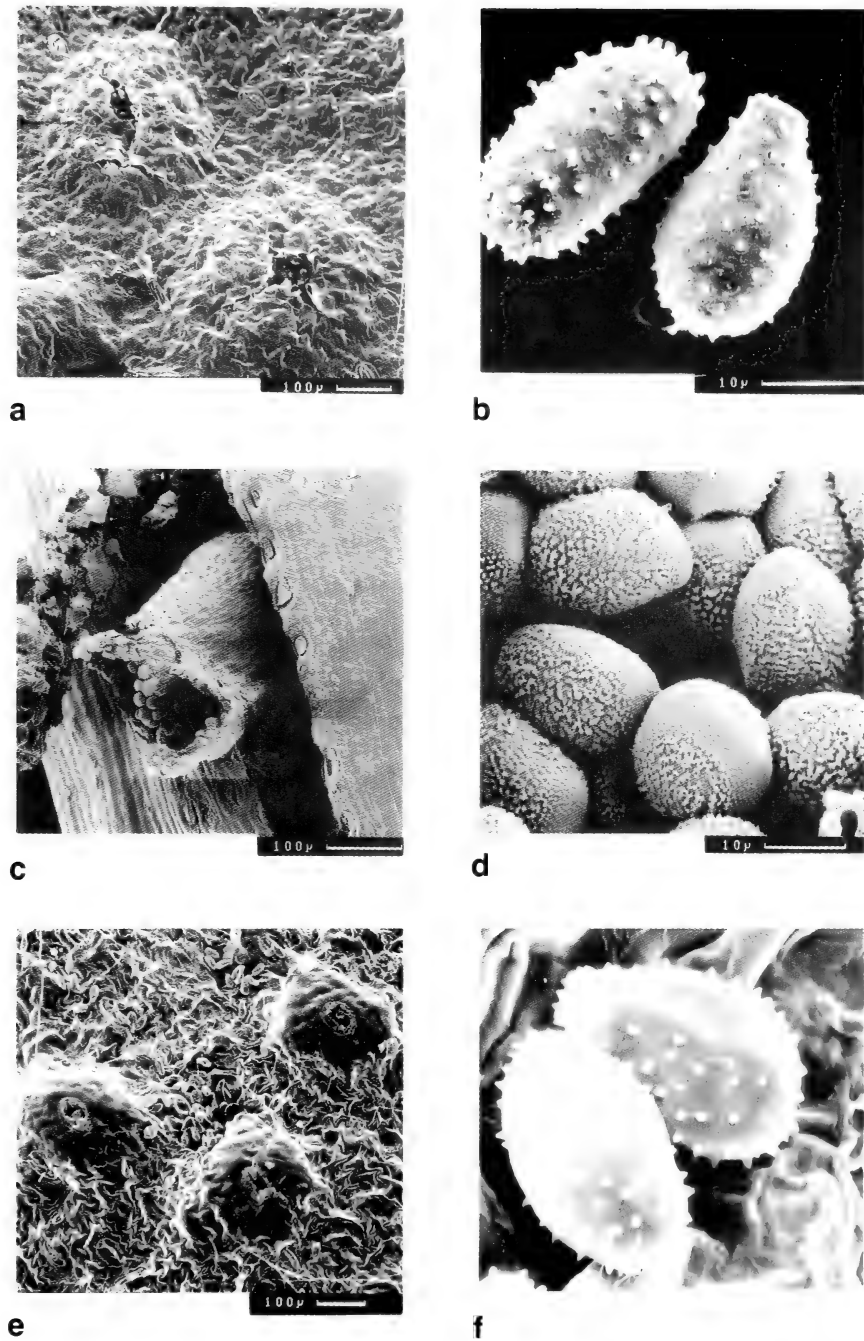
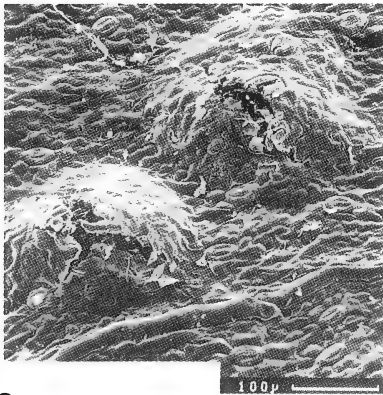
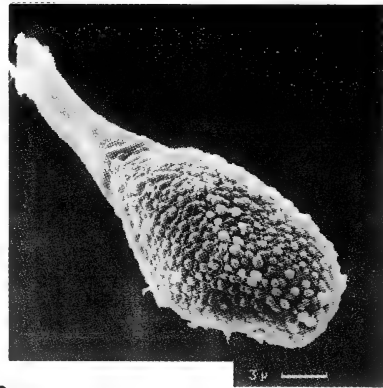


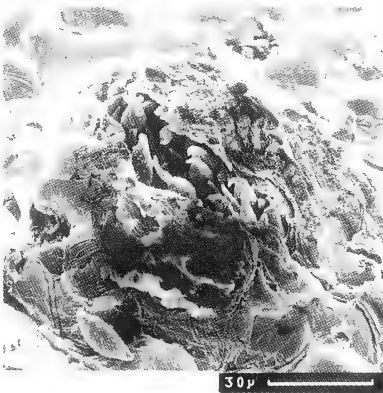
FIGURE 3: *Asplenium scolopendrium* with rust *Milesina scolopendrii*: a) portion of parallel-sided brown area of frond with two rust sori; b) two urediniospores from one of these sori. *Abies alba* with rust *Milesina scolopendrii*: c) aecium on lower surface of needle; d) aeciospores from this aecium. *Polypodium interjectum* with rust *Milesina dieteliana*: e) three rust sori on yellow & brown patch on frond; f) two urediniospores from one of these sori.



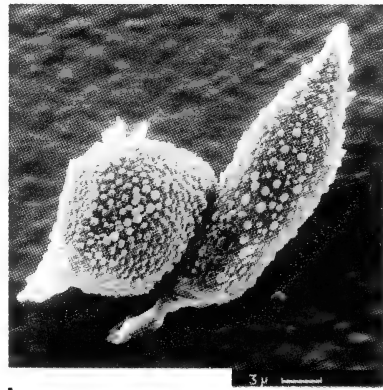
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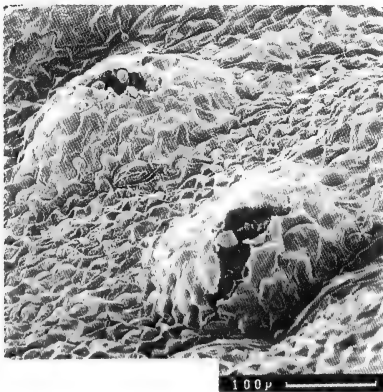
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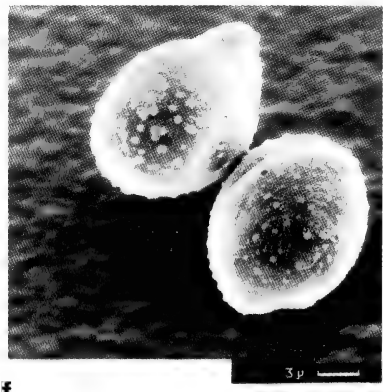
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FIGURE 4: *Phegopteris connectilis* with rust *Uredinopsis filicina*: a) brown portion of frond with two rust sori; b) single thick-walled urediniospore ("amphispore"); c) rust sorus showing elongated urediniospores with apical points; d) one of these normal elongated urediniospores alongside an amphispore, for comparison. *Cystopteris fragilis* with rust *Hyalopsora polypodii*: e) two uredinia from brown portion of frond; f) two urediniospores from one of these sori.

COMMENTS & DISCUSSION ON THE S.E.M. FIGURES

FIGURE 1. *Dryopteris dilatata* – *Abies* rust: *Milesina kriegiana*

All spores are colourless, and often appear like white dust near sori on brown area on fronds. Uredinia shown in the Figure also occur on *Dryopteris filix-mas*, *D. carthusiana* and *D. affinis* (*sensu lato*). The echinulate urediniospores emerge via the centrally placed stoma.

On several *Abies* species, including *A. alba*, the inconspicuous spermatogonia occur most commonly on the upper surfaces of the fir needles, and the aecia occur as shown here in two irregular rows on yellowish parts on the lower surface of the needle. The aeciospores on the fir have distinctly different verruculose ornamentation from the echinulate urediniospores on the ferns. The obscure teliospores occur within the epidermal cells. There are relatively few (easily accessible) records of the occurrence of this common rust e.g. Clark (1980) on *D. filix-mas* from Whichford Wood close to the Warwickshire/Oxfordshire border; Bramley 1985 records it from High Force, Teesdale on *D. dilatata*. See also Preece & Hick, 1989, Atlas species 27. (Sometimes the name *Milesia* is used for *Milesina*, as in this paper. Wilson & Henderson 1966 point out that *Milesia* is the correct term when telia have not been described, and *Milesina* when the teliospores have been described).

FIGURE 2. *Blechnum spicant* – *Abies* rust: *Milesina blechni*

Very similar to *M. kriegiana* but host-specific to *B. spicant*. Aecial stage recorded on *A. alba* and *A. cephalonica*. No recent Warwickshire records (Clark 1980). Bramley (1985) gives only one recent Yorkshire record – near Pickering, 1930. There are older records on *A. pectinata* and *A. amabilis*. As in all British fern rusts, it almost certainly occurs more widely. Wilson & Henderson (1966) say it is “frequent but overlooked” in Britain. See also Preece & Hick, 1989, Atlas species 26.

FIGURE 3. *Asplenium scolopendrium* – *Abies* rust: *Milesina scolopendrii*

Similar to other *Milesina* spp. illustrated here. The stage on the alternate host *Abies alba* seems very rare. There is a record on the fern from Forden in Montgomeryshire in Grove (1913) and it is plentiful on Hart’s-tongue Fern on Llanymynech Hill, Shropshire, in 1989 (T.F.P.).

Though there are no records in Bramley (1985), it has recently been found in Yorkshire (Preece & Hick 1989). One record has been given by Clark (1980) for Warwickshire. Wilson & Henderson (1966) regarded this as a “scarce” rust in Britain. Characteristically, parallel-sided brown-black areas are seen on leaves. In these the raised uredia can be seen as illustrated. See also Preece & Hick 1989, Atlas species 27A.

Polypodium interjectum – *Abies* rust: *Milesina dieteliana*.

As fern taxonomy develops, the rusts of ferns need closer study in the field. Anglesey and Cornish specimens of *Polypodium vulgare* (*sensu lato*) examined in 1989 by one of us (T.F.P.) are certainly *Polypodium interjectum* in the sense of Camus & Jermy (1987). Again regarded by Wilson & Henderson (1966) as a “frequent but overlooked” fern rust species in Britain. The *Abies* stage is either non-existent or very rare. Artificial inoculation experiments have produced aecia on *A. alba* and *A. concolor* (Wilson & Henderson 1966).

Survey work on the different segregates of the *Polypodium vulgare* species could be most rewarding.

FIGURE 4. *Phegopteris connectilis* rust: *Uredinopsis filicina*

The rust genus *Uredinopsis* has long been considered to be the most primitive genus of the *Uredinales*, though this is now disputed (*vide supra*). In general in the genus, the spore walls and spore contents are colourless, and (as distinct from *Milesina*) the obscure teliospores occur in the leaf mesophyll. The uredinia open by tearing of the epidermis (see Figure) as distinct from the stomatal opening as in *Milesina*. There are often two types of urediniospore, thick walled “amphisporae” often polygonal and rounded, and elongated urediniospores with a mucronate tip (see Figure). *Uredinopsis filicina* has not been recorded

on *Abies* in Britain, although it occurs elsewhere on this tree. There have been no Yorkshire records since the 1930's (Bramley, 1985). This is possibly a very rare rust (Wilson & Henderson 1966). See also Preece & Hick (1989) Atlas species 129.

Cystopteris fragilis rust: *Hyalopsora polypodii*

These pictures are of the third and last rust genus so far found in Britain on ferns – *Hyalopsora*. This last genus is generally similar to *Milesina* (see Figure), except there is a pigment in the spore cytoplasm so the spores are yellow when fresh. The obscure teliospores are found in the epidermal cells only and germinate there without winter rest to produce basidiospores. In Yorkshire, at the end of the 19th century, this rust was very common on the fern host in the “fern-cases” beloved of Victorians, as well as in the wild.

It is now it seems rare in the Yorkshire Pennines (Bramley 1985). Grove (1913) drew his illustrations of the fungus from a collection made at Shrewsbury in Shropshire. It seems to be very uncommon in Britain on the Brittle Bladder Fern – but it needs looking for in glasshouses and gardens as well as in the wild. Like *Uredinopsis*, *Hyalopsora* has thick walled “amphisporae” as well as the thin walled normal urediniospores shown on the Figure. It seems that the teliospores have not been seen in ferns in Britain, nor has any alternate aecial stage been found on *Abies*. Wilson & Henderson (1966) point out that in general world wide terms *H. polypodii* has a very wide host distribution and is known on “at least 25 species of fern in 13 genera”. See also Preece & Hick (1989), Atlas species 11.

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SOME ASPECTS OF WATER RELATIONS OF *EQUISETUM TELMATEIA* (EQUISETACEAE: PTERIDOPHYTA)

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ABSTRACT

Diurnal courses of water potential, osmotic potential and pressure potential were studied in the Great Horsetail (*Equisetum telmateia*) growing in a wet alderwood stand (*Carici remotae-Fraxinetum*) in the northern parts of the city of Bochum (North Rhine-Westphalia, FRG). The water relation parameters followed in general the characteristic daily pattern described for flowering plants. Although the watertable was near the soil surface *Equisetum telmateia* was unable to keep a favourable water balance under certain microclimatological conditions (high solar radiation, high vapour pressure deficit) indicating insufficient water uptake and/or transport. A marked but temporary nightly decrease of water potential was observed repeatedly at various times during a two years' study period, a phenomenon for which presently no satisfactory explanation can be given. Methodical problems of determining reliable values for osmotic and pressure potential are briefly discussed.

INTRODUCTION

Little recent research has been done in the field of water relations of pteridophytes. The investigations concentrate on tropical or desert ferns and the influence of droughting on the water balance or gas exchange of those plants (Nobel 1978; Nobel et al. 1978; Eickmeier 1979; Froebe & Strank 1982; Starnecker & Winkler 1982; Sinclair 1983a, 1983b, 1984; Hew 1984; Winter et al. 1986; Nasrulhaq-Boyce & Haji Mohamed 1987). Some ecophysiologicaly orientated work has been done on the hydraulic conductances and the anatomy of xylary elements of different fern species (Woodhouse & Nobel 1982; Calkin et al. 1985; Gibson et al. 1984, 1985).

Detailed data from field measurements focussing on water relation parameters of pteridophytes seem to be not available. In the case of the horsetails (*Equisetum*) this obviously reflects the fact that most species represent wetland or swamp plants and that for these water supply is not regarded as being critical. There is evidence, however, that plants growing in this sort of environment may face specific problems concerning the maintenance of a favourable water balance under large air to leaf water vapour concentration gradients; the low oxygen concentrations in waterlogged soils may be involved herein (cf. Jones 1971; Jones & Muthuri 1984).

Within a more comprehensive research programme to elucidate the ecophysiological adaptations of characteristic species growing in an wet alderwood (Peters 1988) this study concentrates on the daily and seasonal pattern of water relation parameters of *Equisetum telmateia* Ehrh., the Great Horsetail. This species can be a dominant and quite impressive plant in certain vegetation types in Central Europe; its contribution to the production and mineral cycling within these ecosystems is substantial (Peters, unpublished results).

MATERIALS AND METHODS

Study site

Equisetum telmateia was studied at a site situated in the northern parts of the city of Bochum, North Rhine-Westphalia, FRG. On gentle slopes below springs with mainly lateral movement of water a small stand of a semi-natural wet alderwood with dominating black alder (*Alnus glutinosa*) is to be found. This plant community can be classified as *Carici remotae-Fraxinetum* W. Koch (cf. Bennert & Kaplan 1983). The soil represents a base-rich calcareous gley with a pH above 6.0 and a watertable permanently near the surface. Among the herbaceous plants the absolute dominance of *Equisetum telmateia* is most

remarkable. In 1984 about 350,000 shoots of *Equisetum telmateia* were estimated in the whole population covering an area of approximately 5,000 m² (Peters & Bennert 1987).

In 1975 parts of the alderwood was cut down and subsequently a moist meadow as a replacement community with several taxa of horsetails including *Equisetum telmateia* developed. To evaluate the influence of the tree canopy on the water relations of *Equisetum telmateia* a comparison was made between plants growing in the alderwood and those found in the moist meadow.

Measurement of water relation parameters

In 1984 and 1985 monthly investigations of the water relations of *Equisetum telmateia* were carried out during the whole vegetation period. Data of diurnal cycles measured over a period of 24 hours obtained in July and August of both years, 1984 and 1985, are selected here to demonstrate the variability of these parameters. At this time of the year *E. telmateia* is fully developed, towards autumn the tall plants are often damaged and bent by heavy rainfall and storms.

Water potential (ψ_w) measurements were performed in triplicates at intervals of (mostly) 3 hours with a commercial pressure chamber (PMS Instruments, Corvallis, Oregon). Because of the considerable size of the horsetail plants only side branches could be used; these were taken from the upper third of the plants. Simultaneously separate samples for determination of osmotic potential (in duplicates) were harvested and immediately frozen in liquid nitrogen and stored in a deep freezer until further examination. After a short thawing period (5 min) sap was expressed from this plant material with a specially constructed press (Kreeb 1977) and used for determination of the osmotic potential (ψ_s) employing the cryoscopic method (KNAUER Semi-Micro Osmometer, type M). Each sap sample was analysed twice. The values of osmotic potential (ψ_s) and water potential (ψ_w) were used to calculate the corresponding pressure potential (ψ_p).

Microclimatological measurements

Air temperature and relative air humidity were monitored with a hygrothermograph. From these data vapour pressure deficit (VPD) was calculated. Total short wave radiation was registered with a bimetallic actinograph which was placed on the wet meadow neighbouring the forest.

RESULTS

Both days in July (25.7.1984 and 24.7.1985) that had been chosen for measurements were warm and sunny with maximum temperatures of 22° to 23°C (figs. 1A and 2A). Solar radiation reached a maximum value of approximately 4.5 J/cm² · min on both days (figs. 1B and 2B). In early afternoon VPD rose up to 13 mbar (figs. 1C and 2C). Starting from high predawn values (-1 to -2 bar), the water potential decreased more or less slowly during the morning to reach its lowest values of -6 to -7 bar around midday (figs. 1D and 2D). In the following hours water potential recovered gradually. In July 1984, in spite of a relatively high VPD, water potential did not drop below -5.5 bar (fig. 1D) whereas in 1985 under similar conditions -7.5 bar were reached (fig. 2D). In both years a more or less distinct but temporary decrease of water potential during night time was observed. The osmotic potential followed generally the course of water potential although its diurnal variations were less significant. Especially in July 1985 (fig. 2D) it showed only small changes within the range of 1 bar. Pressure potential reached its lowest values around noon; in 1984 it decreased to only 0.5 bar.

The 16th of August 1984 (fig. 3) was a mainly sunny and warm day which fell into a fairly dry time of year – it had not rained for the previous 11 days. In the early afternoon values of VPD exceeded 10 mbar. The 26th of August 1985 (fig. 4) was colder with a maximum temperature of only 16°C and a fairly high degree of air humidity (VPD permanently

under 3 mbar). During day time hours water potentials again reached their minima around noon (figs. 3D and 4D); especially low values (-11.5 bar) were recorded in 1984. In 1984 patterns of variation in osmotic potential paralleled those in water potential; in 1985 it showed only minor diurnal fluctuations. In both years the course of pressure potential was substantially influenced by that of the water potential. In 1984 a water potential lower than the osmotic potential was determined around noon and a negative value of pressure potential resulted (fig. 3D).

Fig. 5 shows results obtained on 26th August 1985 when for comparison additionally plants of *E. telmateia* were measured that were growing on the neighbouring open moist meadow. The most obvious difference to the forest plants is to be found in water relation parameters around noon and in early afternoon. In the open habitat much lower (more negative) values of water potential (-9.5 versus -5 bar) occurred with pressure potential approaching zero. In both habitats water potential showed a remarkable nightly decrease (at 0200 h) for which no explanation can be deduced from microclimatological data.

DISCUSSION

Comparative results of water relation characteristics and their diurnal variations in pteridophytes and especially horsetails obtained from field measurements are obviously not reported in literature. However, the degree of diurnal cycling as well as the values of water-, osmotic-, and pressure potential of *Equisetum telmateia* lie well in the range determined for many herbaceous flowering plants (e.g. Lösch & Franz 1974; Richter 1976; Curtis & Kincaid 1984; Grimme 1984), especially for those from wetland communities (Richter 1976; Larcher 1984).

Plant water status fluctuates diurnally under variable microclimatological conditions. The interactions of environmental factors like temperature, relative air humidity, wind velocity, vapour pressure deficit and solar radiation, which change spatially and with time, are difficult to establish (Elfving et al. 1972). In many cases the daily course of water potential mirrors the diurnal variation of radiation, which, besides VPD, is often regarded as having the strongest effect (Huzulak 1977; Pereira & Kozłowski 1978; Grimme 1983).

The most striking result was the obvious difficulty *Equisetum telmateia* faced occasionally when trying to keep a favourable water balance. This became obvious in a sharp decrease of water potential with pressure potential approaching zero (or even being estimated as negative) and occurred even under rather moderate environmental conditions, but always around noon when air temperature and solar radiation reached their daily maximum. As the high watertable of the studied alderwood ecosystem indicates that water was freely available to the roots of *Equisetum telmateia* water shortage in the soil cannot be responsible for this phenomenon. Calkin et al. (1985), examining the water conduction of xylem elements of different fern species, found in some of them the tracheids partially blocked. Although horsetails were not included in these studies, the temporary drop of water- and pressure potential in *Equisetum telmateia* is more likely to be caused by insufficient water conduction or uptake rather than reduced water availability. Additional support for this explanation can be derived from studies on water relations of certain flowering plants. When their roots were subjected to flooding conditions, thereby experiencing anaerobiosis, resistance to water flow through roots and stem increased indicating partial occlusion of the xylem vessels (Andersen et al. 1984).

On the other hand water potential recovered fairly quickly in the course of the afternoon (see esp. figs. 3 and 5), a process to which also a partial closure of stomata could have contributed. Data obtained by Peters (1988) in other years show that *Equisetum telmateia* indeed tends to reduce stomatal opening and transpiration rate early in the afternoon under conditions of intensive insolation and high vapour pressure deficit of the air occurring during summer months. Midday closure of stomata was observed repeatedly, both, in well watered

shrubs and food plants under experimental conditions (Lange & Meyer 1979; Lange et al. 1982) and in naturally growing wetland plants (Jones 1971; Jones & Muthuri 1984). Whereas Lange & Meyer (1979), interpreting their results obtained in apricot and grapevine, regard midday depression of stomatal conductance in plants sufficiently supplied with water from an ecological point of view as unnecessary and even disadvantageous, Jones & Muthuri (1984) give a quite different explanation. Examining the behaviour of plants of a papyrus (*Cyperus papyrus*) swamp in Africa, they propose that the reduction of water flow into the roots at high atmospheric demand is directed at reducing the uptake of toxic ferrous iron. These iron compounds as well as other toxic elements (especially Mn^{2+}) are abundant under anaerobic and reducing soil conditions of many wetland ecosystems (cf. Crawford 1982; Wheeler et al. 1985; Janiesch 1986). According to Peters (1988) this applies also to the soil of the alderwood stand where the investigated *Equisetum* plants were growing.

In all cases a more or less obvious temporary decrease in water potential occurred during night, mostly between midnight and 0300 h. Such nightly fluctuations have now been observed over a period of two years, occurring rather frequently but irregularly. One possible explanation to be considered is that a transitory phase of reopening of stomata during night time causes increasing transpiration rates which in turn could result in a drop of water potential. However, recent investigations on *Equisetum telmateia* do not support this possibility. Peters (1988) could demonstrate that stomata of *Equisetum telmateia* often are kept open to a certain degree during the whole night and that transpiration rate is very low because of high air humidity in the alderwood stand. Neither in stomatal opening nor in transpiration rates were observed nightly changes that could explain a decrease of water potential in the magnitude of 2 to 3 bar. It is remarkable that also alder (*Alnus glutinosa*) plants from the same habitat exhibited a nightly decrease of water potential, however, somewhat less frequent than *Equisetum telmateia*, but again without any indications that changes of stomatal opening and in transpiration rate might be involved (Peters 1988). In literature, nightly changes in plant water status is rarely reported or commented on (Hinckley 1971; Elfving et al. 1972; Hinckley & Ritchie 1973; Cutler et al. 1977). Rather well known for many years has been the fact that stomata sometimes open in the dark, a phenomenon usually termed "night opening". It is commonly believed to be related to an endogenous rhythm, but it can also be substantially enhanced by higher temperatures (e.g. Mansfield 1965; Pemadasa 1977). Occasionally the night opening was interpreted as being caused by a shortage of oxygen within the plant (Scarath et al. 1933; Levitt 1976) and termed "scotoactive opening".

Under certain microclimatological conditions a water potential more negative than the corresponding osmotic potential was measured and consequently a negative pressure potential was calculated. Although the existence of negative turgor is regarded as possible by several investigators (e.g. Grieve 1961; Kreeb 1960, 1961; Kappen et al. 1972; Beadle et al. 1978) it has never been established with certainty whether - with continuing dehydration - pressure potential of cells or tissues remains zero or indeed turns negative. What, however, has been demonstrated repeatedly is that negative pressure potentials may result as an artefact if the (absolute) value of the osmotic potential is underestimated (cf. Tyree 1976). This is normally the case when employing the cryoscopic method as during preparation of sap the separation between symplasmatic water (containing solutes) and apoplasmatic water (relatively pure water contained in the cell wall) is abolished and both fractions are mixed. As a result the cryoscopically measured osmotic potentials are generally too high (their absolute values too low). Cutler et al. (1977) report errors up to 45%; Markhart et al. (1981), using filter paper as model systems, predict errors between 10 and 40%. Therefore the negative pressure potential found in *Equisetum telmateia* must be understood as caused by the cryoscopic method employed. But even if the recorded negative pressure potential is regarded as unrealistic it indicates that *Equisetum* suffers from (at least moderate) water

FIGURE 1: Diurnal course of microclimatological parameters and water relation components of *Equisetum telmateia* (alderwood stand) on 25 July 1984. A: Air temperature (T). B: Total short wave radiation (St). C: Vapour pressure deficit (VPD). D: Water relation parameters; \blacktriangle : water potential; \bullet : osmotic potential; \circ : pressure potential.

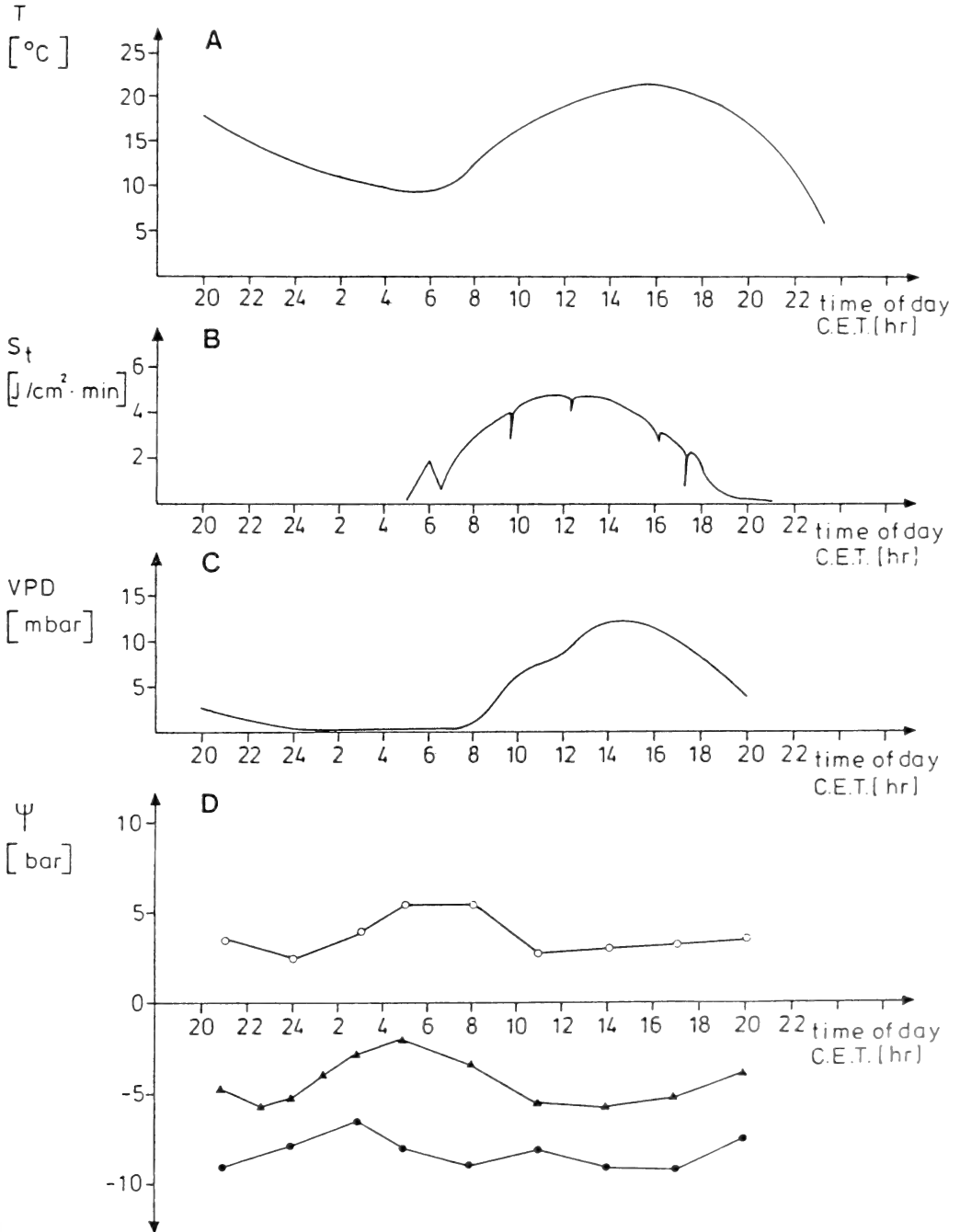


FIGURE 2: Diurnal course of microclimatological parameters and water relation components of *Equisetum telmateia* (alderwood stand) on 24 July 1985. A: Air temperature (T). B: Total short wave radiation (St). C: Vapour pressure deficit (VPD). D: Water relation parameters; \blacktriangle : water potential; \bullet : osmotic potential; \circ : pressure potential.

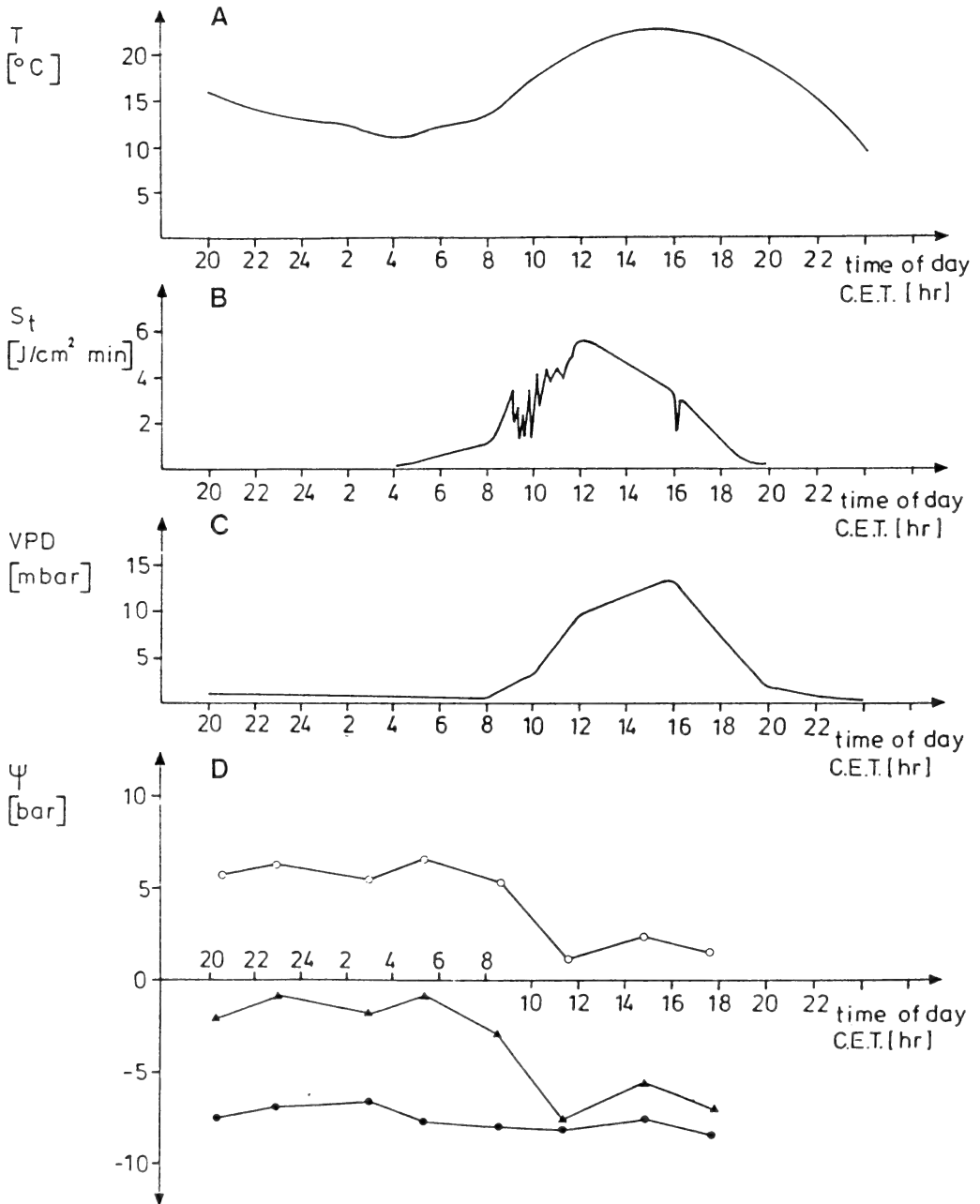


FIGURE 3: Diurnal course of microclimatological parameters and water relation components of *Equisetum telmateia* (alderwood stand) on 16 August 1984. A: Air temperature (T). B: Total short wave radiation (St). C: Vapour pressure deficit (VPD). D: Water relation parameters; ▲ : water potential; ● : osmotic potential; ○ : pressure potential.

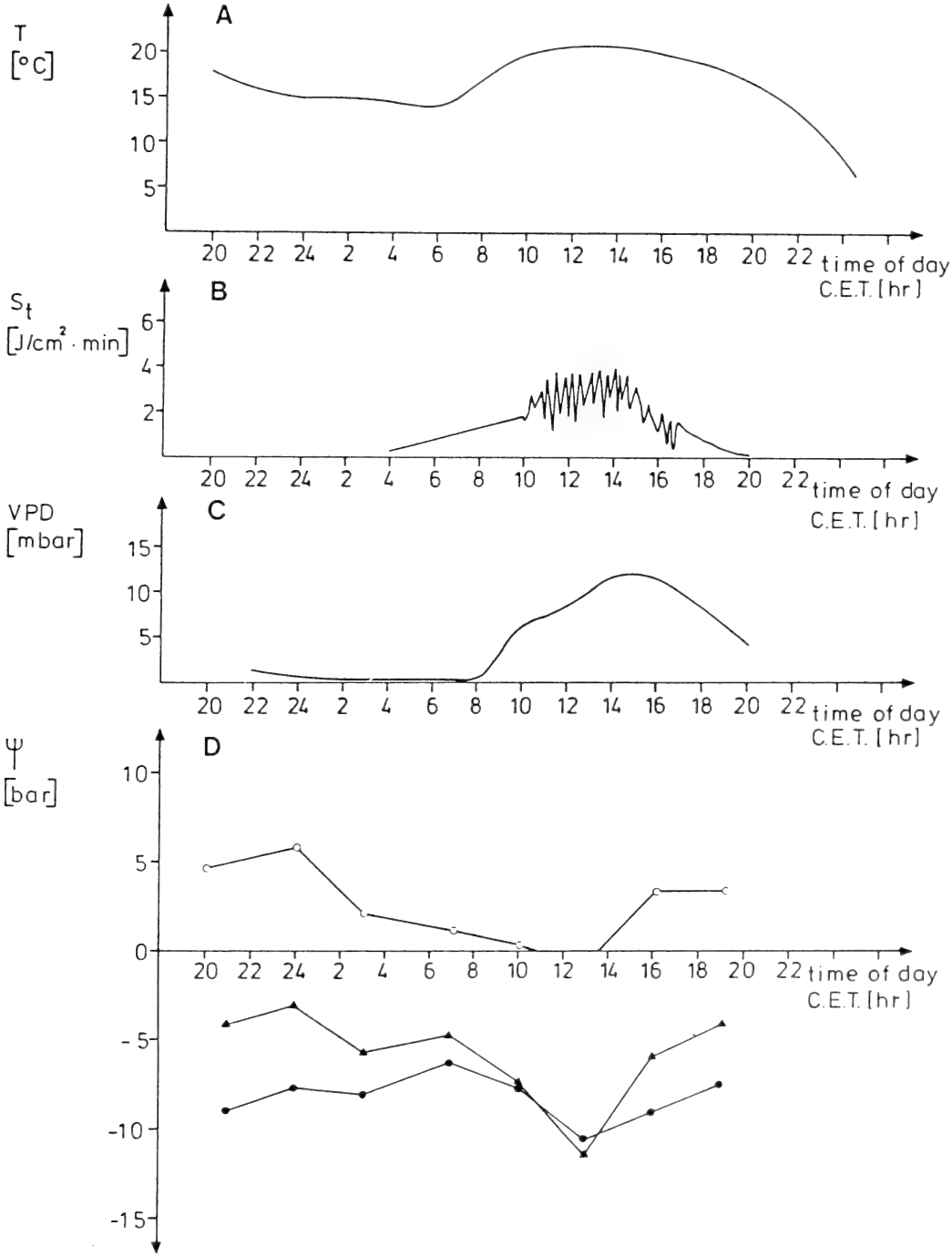


FIGURE 4: Diurnal course of microclimatological parameters and water relation components of *Equisetum telmateia* (alderwood stand) on 26 August 1985. A: Air temperature (T). B: Total short wave radiation (St). C: Vapour pressure deficit (VPD). D: Water relation parameters; ▲ : water potential; ● : osmotic potential; o : pressure potential.

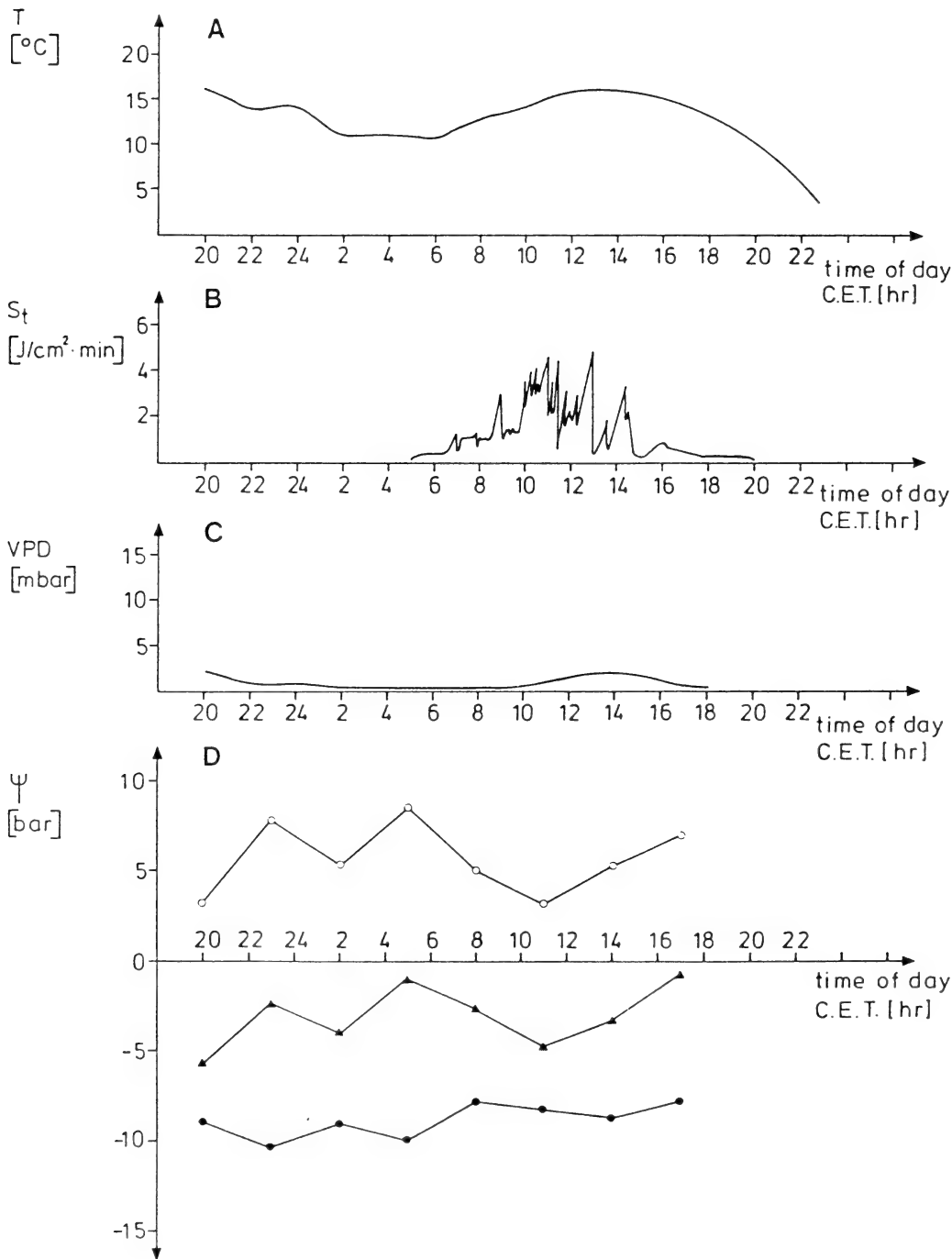
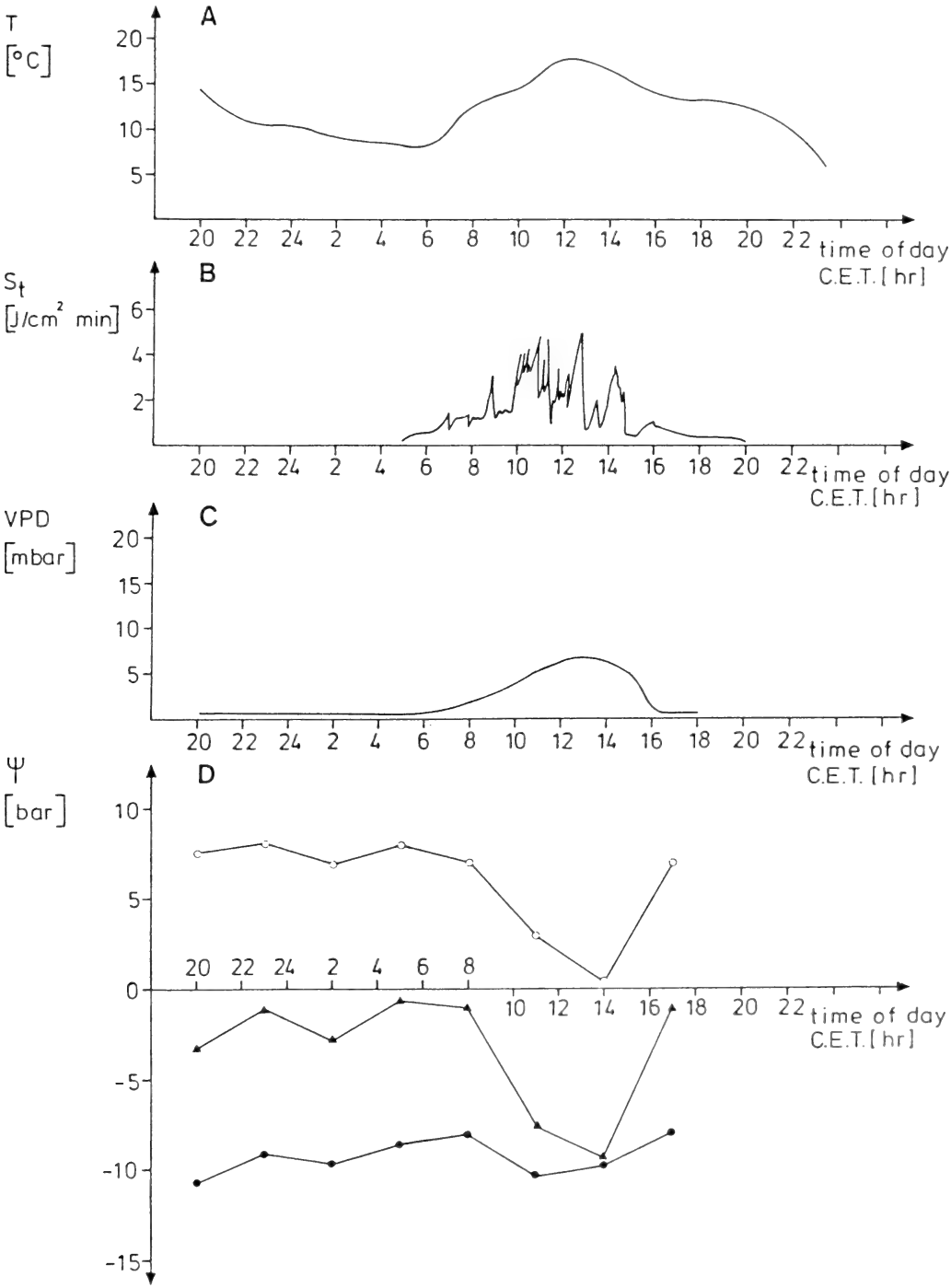


FIGURE 5: Diurnal course of microclimatological parameters and water relation components of *Equisetum telmateia* (moist meadow) on 26 August 1985. A: Air temperature (T). B: Total short wave radiation (St). C: Vapour pressure deficit (VPD). D: Water relation parameters; : water potential; : osmotic potential; o : pressure potential.



stress under high atmospheric demand.

Repeatedly another method, the so-called pressure-volume curve technique (see Tyree & Hammel 1972 and Ritchie & Hinckley 1975 for details), was successfully applied to different plant species yielding more realistic values of osmotic potential (e.g. Kaplan & Gale 1974; Roberts & Knoerr 1977; Cutler et al. 1979; Roberts et al. 1980; Clayton-Greene 1983). Unfortunately, it could not be used in the case of *Equisetum telmateia* because of the inner cave system of the stems and branches which tends to collapse if high pressure is applied. Occasionally values of osmotic potentials obtained by pressure-volume curves were used to calculate a correction factor for those determined by cryoscopy (cf. Bennert & Mooney 1979). Peters (1988) and David (unpublished results) were able to determine such a correction factor for *Fraxinus excelsior*, *Alnus glutinosa* and *Epilobium hirsutum* growing in or near the studied alderwood stand. It amounted to 3 to 4 bar depending on the species under examination. Provided that a factor of the same magnitude would also be applicable to *Equisetum telmateia* at no time would a negative turgor really occur in this species.

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THE CHROMOSOME NUMBER OF *ANOGRAMMA LEPTOPHYLLA* (ADIANTACEAE: PTERIDOPHYTA) FROM EUROPE

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ABSTRACT

Meiotic counts in spore mother cells of *Anogramma leptophylla* are reported for plants from seven origins: Madeira (2), France (2), Continental Spain (1), Mallorca (1) and Switzerland (1). We invariably found $n = 26^{II}$ in agreement with the questionable count of Tutin in Fabbri (1963), Kurita (1971) and Queiros et al. (1988), (all three for material from Europe) and Gibby (1986, material from Madeira). These results are, however, in disagreement with Brownlie (1958, $n = 29$, material from New Zealand), Mickel et al. (1966, $n = 27$ and 29 , from Mexico), Baroutsis & Gastony (1978, $n = 29$, from S. Africa), and Mehra & Verma (1960, $n = c. 56-57$), Verma & Khullar (1965, $n = c. 58$), and Khullar in Manton et al. 1986:130, $n = 58$ plants from India. On the other hand we found $n = 29^{II}$ for *Anogramma chaerophylla* (precise origin unknown) in agreement with Walker (1966) and with Gastony & Baroutsis (1975). The genus *Anogramma* is obviously cytologically not homogeneous.

INTRODUCTION

We became interested in the chromosome number of *Anogramma leptophylla* (L.) Link (1841:1377) when the late Irene Manton wrote to one of us (T.R. in litt. 26th June 1985) that in order to complete manuscript on "Cytology of the fern Flora of Madeira" (Manton et al. 1986) she urgently needed precise chromosome numbers of *Anogramma leptophylla* and of *Notholaena marantae* (L.) Desv. subsp. *subcordata* (Cav.) Kunkel (1969:46). We were able to provide one for the *Notholaena* (Manton et al. 1986: 138) but were too late for *Anogramma* which we raised from spores from Madeira. Fortunately Mary Gibby was able to obtain fixings collected in the field, and she found $n = 26^{II}$ (Manton et al. 1986:131, foot note, and Mary Gibby 1986). This agrees with the questionable count of Tutin in Fabbri (1963: 323), with the results of Kurita (1971: 41-42), and with the recent count of Queiros et al. (1988:124) for material from Europe. It is, however, in contrast with counts of other workers who reported $n = 29$ for material from New Zealand (Brownlie (1958); $n = 27$ and 29 for material from Mexico (Mickel et al. 1966); $n = 29$ for South Africa (Baroutsis & Gastony 1978) and $n = 58$ for India (Verma & Khullar 1965, see Khullar in Manton et al. 1986: 130). These results and counts of other species of *Anogramma* are reviewed by Gastony & Baroutsis (1975); Baroutsis & Gastony (1978); Löve et al. (1977:142-143); Manton et al. (1986:130-131); and by Gibby (1986). We therefore decided to continue raising plants from spores and collecting fixings in the field of different origins, particularly Europe, to determine their chromosome numbers. For comparison we included a specimen of *Anogramma chaerophylla* (Desv.) Link (1841:138).

The chromosomes of *Anogramma* have proved difficult to study (reviewed by Manton et al. 1986:130-131); they are minute, often exhibit stickiness and have a tendency towards clumping; the presence of B-chromosomes has occasionally been reported. We encountered similar difficulties, but whenever ample, good fixings were available, several well spread cells always could be found. We observed neither B-chromosomes nor fragments. The precautions which we used for fixings taken in the field, to avoid deterioration during subsequent transport, are described below.

Anogramma leptophylla is often described as an annual and sometimes as annual to biennial (Dostál in Kramer 1984:113). In our experiments it usually behaved as biennial (details see sowing TR-6336, spores from Madeira). Spores sown in December 1985 gave ample prothalli which were planted in soil in Febr. 1986. They grew fast, covered the pot soon, but died down in May-June. Only in the fall of 1986 did many young sporophytes come up on the brownish mat, probably from underground tubercles (Goebel 1877). These tubercles must obviously have been formed after fertilisation and before the gametophytes died down. Mature leaves and fixable sori became available in April 1987. Many other sowings made in Jan. 1989 (not further reported here) with spores from Spain, France and Italy also died down in summer 1989. In some cases a few gametophytes remained green till autumn and through the whole next year, but never produced mature sporophytes until a full year had elapsed after sowing. The behaviour of *A. leptophylla* as annual or biennial may depend on growing conditions and season of spore germination, but in our experiments it always behaved as biennial.

MATERIAL AND METHODS

Spores or fixings collected in the field of *Anogramma leptophylla* were used from the six following origins (registration numbers T.R. are given for the living progeny).

1. (TR-6336) = R. Viane 3063, (Fig. 1) 11th July 1985, Madeira, roadside between Gaula and Aguas Mansas, below the Pico das Eirozes, c. 740 m alt. Together with *Adiantum reniforme* L., *Asplenium obovatum* Viv. subsp. *lanceolatum* P. Silva, *A. onopteris* L., *Ceterach ilegnamense* Gibby & Lovis (1989:287), *Polystichum setiferum* (Forsk.) Woyнар.



FIGURE 1: Silhouette of pressed frond of plant TR-6336 = *A. leptophylla* raised from spores from Madeira (pressed 1st June 1987).

2. (TR-6337) = R. Viane 3050, 10th July 1985, Madeira, Curral das Freiras, roadside wall falling apart, c. 650 m alt. Together with *Asplenium onopteris*.
3. (RAS-608 = fixing coll. in the field). W. Bennert, H. Rasbach & K. Rasbach 15th April 1988, Spain, Prov. Cádiz, Miel Valley (W. of Algeceiras), c. 90 m alt.
4. (R.V.-4512 : fixing coll. in the field). R. Viane 3rd April 1989, Switzerland, Kt. Ticino, Valle Maggia, at the left side of the small, old track from Bignasco (442 m) to Madonna del Monte (734 m) at c. 550 m alt. under trees. One of the few long known localities in Switzerland.
5. s.n. fixed in the field. W. Bennert s.n. 5th April 1989, France, Dépt. Alpes-Mar. Rocher de Roquebillière near Cannes, c. 110 m alt., in open situation between bushes.
6. s.n. fixed in the field, W. Bennert s.n. 7th April 1989, France, Dépt. Var, Ile de Port-Cros (Iles d'Hyères), at c.50 m alt., slope beside a path.
7. (TR-6995) = J.A. Roselló, s.n. 13th April 1989, Balearic Islands, Mallorca, près de Caimari, dans les crevices des talus ombragés sur calcaire (in litt. 14th April 1988).
8. (TR-7041) = *Anogramma chaerophylla*. On 3rd March 1988. Mr R. Schweizer (Strengelbach, Switzerland) sent us some living prothalli of this species which he had cultivated for some time in his greenhouse. They came up as a weed, in pots with orchids which he had received from a commercial dealer and from friends. The precise origin is unknown but they came from tropical America, perhaps from Venezuela, Bolivia, Ecuador or Peru. For determination of a fertile plant he is grateful to Prof. K.U. Kramer (Z). A photograph of a plant cult. in Basel is given in Fig. 2.



FIGURE 2: Silhouette of pressed frond of plant TR-7041 = *A. chaerophylla* grown from material (gametophytes and small sporophytes) obtained from R. Schweizer (pressed 8th July 1985).

For fixation juvenile leaves with immature, slightly swollen, whitish sporangia were used. If some brownish or blackish points (mature spores) were visible on the lowest pair of pinnae, the upper part of the leaves was sometimes still in usable state. A leaf, or part of it, was immersed into a solution of 1:3 glacial acetic acid: absolute ethanol, freshly mixed in a glass tube with plastic stopper and a small label written with pencil (graphite) included. If possible these fixings were kept at c. 0-4° C in a thermos bottle with ice (in the field) or in the refrigerator at home. After c. 1-5 days the liquid was replaced by fresh mixture and the fixings were stored at c. -15° C in the deep-freezer until they could be examined cytologically. If this was not possible or if the fixings had to be mailed for a journey taking more than 3 days, the liquid was replaced by 70% aqueous ethanol. This gave sometimes quite acceptable results after being kept protected from light up to 2 months at room temperature.

The technique described by Manton (1950:293-299) was followed for squashing spore mother cells in meiosis, staining in aceto carmine and preparing permanent slides. Suitable cells were examined and analysed in phase-contrast on an "Olympus" microscope model BH 2 with oil immersion and attachment for phase contrast (by H.R.).

Plants were raised from spores (by T.R.) on agar medium. The medium given in A.F. Dyer (1979:282) was used with slight modification (adding NaCl). The following quantities are for one litre:

0.51 g crist. Magnesium sulphate = $\text{Mg SO}_4 \bullet 7 \text{ H}_2\text{O}$

0.12 g Potassium nitrate = KNO_3

0.17 g crist. Ferric chloride = $\text{FeCl}_3 \bullet 6 \text{ H}_2\text{O}$

1.44 g crist. Calcium nitrate = $\text{Ca(NO}_3)_2 \bullet \text{H}_2\text{O}$

0.25 g Potassium dihydrogen phosphate = KH_2PO_4

0.10 g Sodium chloride = NaCl

16.00 g Agar powder

The salts are each dissolved in c. 10 ml clean tap water, added in the given order to c. 600 ml tap water, rinsed and filled up to make one litre. We added trace elements (Döpp 1973:3-4; Reichstein et al. 1973:135). No Mycostatin was added. The mixture was heated in a round bottle flask (on the steam bath) with occasional stirring for c. one hour. The slightly turbid homogeneous solution was poured in c. forty Erlenmeyer flasks 65 mm diameter to make a c. 15 mm thick layer. The flasks were covered with tinfoil, sterilized in steam (100°C) for twenty minutes and covered tight with "parafilm M" (plastic). They can be stored for a year in this condition. If an infection becomes visible, the flask can be sterilized again. Prothalli when 2-3 mm high, were pricked out in pots with lime free mixture (Rasbach et al. 1983:45).

PLANTS RAISED FROM SPORES

We give two examples showing slightly different behaviour of prothalli:

1. TR-6336, spores from Madeira. Sowing on Agar-medium 7th Dec. 1985; pricking of prothalli on soil in one pot 12th Febr. 1986. The prothalli were covered with a plastic cup and sprayed daily. They grew well and soon covered the whole surface of the pot. They became brown in c. June 1986 and were then kept as before covered in the humid greenhouse atmosphere, but not watered. We started to spray again on 1st Nov. 1986 and young sporophytes soon started to grow out of the brown mat. Twelve of them were planted in single pots kept covered for a few days, then uncovered in the greenhouse (6-20°C)

and sprayed daily. Ten plants survived. Mature leaves and good fixings were available on 13th Apr. 1987, i.e., 16 months after sowing and after a resting period. Fig. 1 shows two fronds of a mature plant.

2. TR-6995, spores from Mallorca sown 26th Apr. 1988 on Agar-medium gave ample prothalli which were pricked out on soil on 19th Sept. 1988. They grew well and most decayed again in c. Nov. 1988, but some remained green throughout 1989 and are still green (Febr. 1990). The first sporophytes could be potted on 6th July 1989. Good fixings were made, fronds were available on 11th Jan. 1990. We did not check whether the sporophytes came from the green prothalli or from tubercles of decayed ones.

Most of the sowings (made in Jan. and Apr. 1989, not reported here) behaved like TR-6336 i.e. dying down completely in summer, but in a few cases some prothalli remained green as TR-6995. Fertile sporophytes were never available within a period of one year from sowing.

ANOGRAMMA CHAEROPHYLLA

TR-7041. As mentioned, Mr Schweizer (with litt. of 3.3.1988) provided us with a clump of small sporophytes (weeds on orchids) which were potted immediately. After eliminating some other weeds (*Pteris*, *Dryopteris*) we were able to raise 3 specimens of the *Anogramma* (det. by Prof. K.U. Kramer, Z). Mature leaves (Fig. 2) and good fixings were available on 3rd Apr. 1989, a whole plant was pressed on 8th July 1989.

CYTOLOGY

Five of the seven specimens of *A. leptophylla* (listed above) gave precise results with $n = 26^{II}$ in meiosis. Specimen TR-6337 (from Madeira) was not examined, because two other specimens (including the result of M. Gibby) have already been counted and $n = 26^{II}$ was found. Specimen 5 (W. Bennert s.n. near Cannes) did not yield any good cells and only an approximate count $n = c. 26^{II}$ ($\pm 1-2$, surely not 29) could be obtained. Figs. 3-4 give photographs and explanatory diagrams for the five mentioned specimens. Fig. 5 gives similar illustrations for our material of *A. chaerophylla* showing $n = 29^{II}$.

DISCUSSION

The name *Anogramma leptophylla* (L.) Link (1841:137) is based on *Polypodium leptophyllum* Linnaeus (1753:1092). A lectotype for this name was designated by Morton (1970:101-103) and met with general acceptance. It is specimen number 1251156 in LINN. It bears the name *Polypodium heterophyllum* in Linnaeus' hand and the number 46. As Pichi Sermolli (1966:496-595) pointed out, Linnaeus called it this before realizing that he had already applied the name *P. heterophyllum* to another species, and published it as *P. leptophyllum*. Linnaeus (1753:1092) gives: "Habitat in Hispania, Lusitania, Galloprovincia". We have examined material from all three of these countries and found them to have $n = 26^{II}$. We therefore conclude that this is the correct number for *A. leptophylla* s.str.

There remains the problem of the plants from New Zealand, S. Africa and India for which $n = 29^{II}$ has been reported. It would be desirable to check these results. So far, we were able to obtain spores from N.India (S.P. Khullar). They gave some prothalli, but no sporophytes were produced. We were not able to obtain material from N.Z. and from S.Africa. If the reported counts ($n = 29^{II}$) are correct, such material would have to be treated as an aneuploid or as a distinct taxon.

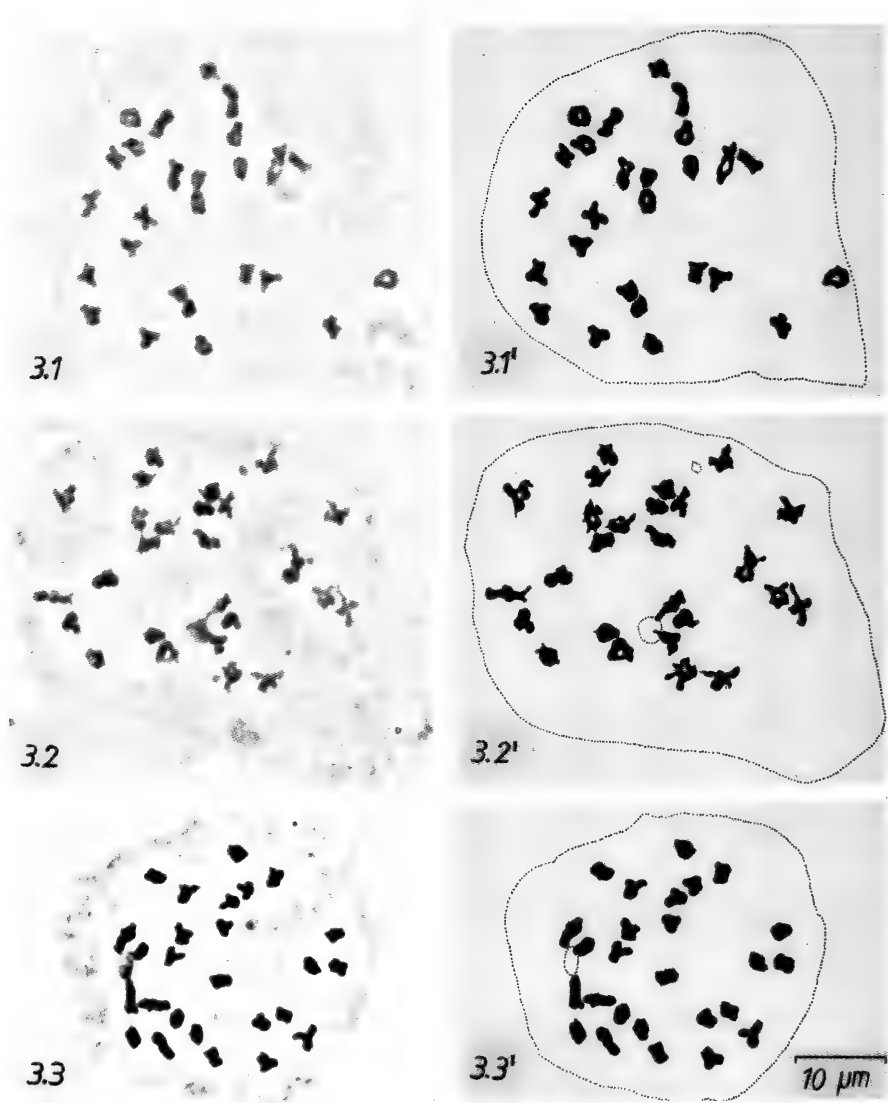
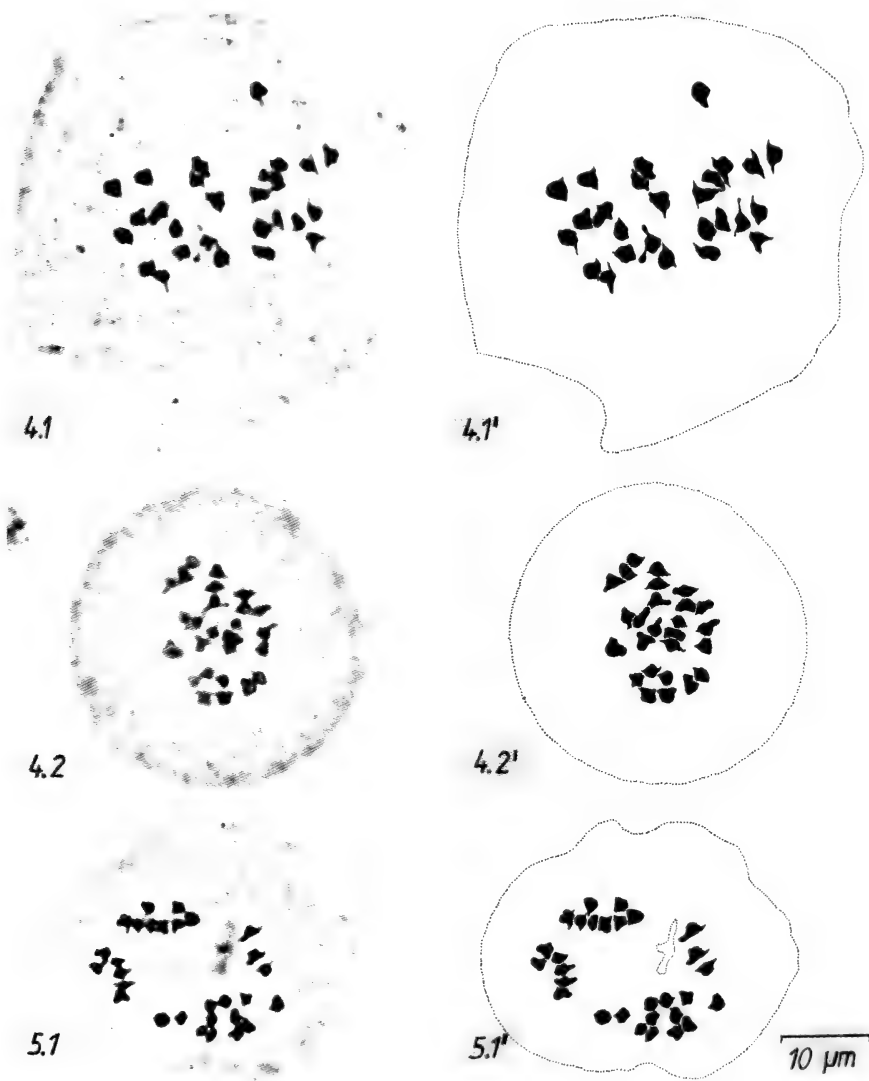


FIGURE 3: 3.1, 3.2 and 3.3 = photographs, 3.1', 3.2' and 3.3' = explanatory diagrams of spore mother cells in meiosis of *A. leptophylla*: 3.1 and 3.1' = TR-6336 raised from spores from Madeira, in diakinesis showing $n = 26^{II}$; 3.2 and 3.2' = Ras-608 fixed in the field, Miel Valley, Spain, in diakinesis showing $n = 26^{II}$; 3.3 and 3.3' = RV 4512 fixings collected in the field from Switzerland, in metaphase I showing $n = 26^{II}$.



FIGURES 4 and 5 (continuation of Fig. 3): 4.1. and 4.1' = *A. leptophylla* fixings collected in the field, W. Bennert s.n. from Ile de Port-Cros, France, in metaphase I showing $n = 26^{II}$; 4.2 and 4.2' = TR-6995 = *A. leptophylla* ex spores from Mallorca, in metaphase I showing $n = 26^{II}$; 5.1 and 5.1' = *A. chaerophylla* from Central- or S. America, cell in metaphase I showing $n = 29^{II}$.

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***ASPLENIUM* × *ARTANENSE* (ASPLENIACEAE: PTERIDOPHYTA)
A NEW DIPLOID HYBRID FROM MALLORCA, SPAIN**

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ABSTRACT

A new *Asplenium* hybrid from Mallorca (Artá) is here described and named as *Asplenium* × *artanense* Rosselló, Cubas, Gradaille & Sastre. This hybrid is diploid showing up to 72 univalents at meiosis. The cytological results, as well as the morphological characteristics and ecology of this plant, strongly suggest that it originated from a cross between *A. sagittatum* and *A. trichomanes* subsp. *inexpectans*.

INTRODUCTION

The European species of Aspleniaceae have been ascribed to either five different genera: *Asplenium* L., *Phyllitis* Hill, *Ceterach* DC., *Phyllitopsis* Reichstein and *Pleurosorus* Fée (Pichi Sermolli 1977, 1987; Reichstein 1981; Ferrarini et al. 1986) or to a single genus: *Asplenium* (Jermy 1968; Lovis & Vida 1969; Salvo et al. 1982; Derrick et al. 1987). Accordingly with the adopted taxonomic position, the natural hybrids between species of *Phyllitis* and *Asplenium* have been named either as intergeneric (× *Asplenophyllitis* sp.) or as intrageneric hybrids (*Asplenium* × sp.). Since the existence of these hybrids demonstrates that these two groups are not completely genetically isolated (Lovis & Vida 1989), we consider that there are no strong reasons for splitting *Asplenium* into different genera, and therefore all the European taxa of Aspleniaceae are here treated as belonging to a single genus: *Asplenium*.

A. scolopendrium L. and *A. sagittatum* (DC.) A.J. Bange are diploid species (Manton 1950), and probably both of them are descendants from a common ancestor (Emmott 1964). *A. scolopendrium* is known to have crossed with *A. trichomanes* L. subsp. *quadrivalens* D.E. Meyer, *A. adiantum-nigrum* L., *A. obovatum* Viv. subsp. *lanceolatum* P. Silva and *A. lepidum* C. Presl subsp. *lepidum*, thus originating four wild triploid hybrids named: *A. × confluens*, *A. × jacksonii*, *A. × microdon* and *A. kummerlei* (Vida 1963; Girard & Lovis 1968; Lovis & Vida 1969; Lovis 1975).

The related species *A. sagittatum* is involved in the origin of *A. hybridum* (Milde) A.J. Bange (= *Phyllitopsis hybrida* (Milde) Reichstein), an allotetraploid species whose parentage is *A. sagittatum* and *A. ceterach* L. subsp. *bivalens* (D.E. Meyer) Greuter & Burdet (Vida 1963; Emmott 1964). Apart from this fertile species, only one hybrid involving *A. sagittatum* as one of the parents has been described till now in Europe: *A. × dutartrei*. Based on its morphological characteristics, this hybrid has been considered to be the cross between *A. sagittatum* and *A. ceterach* subsp. *ceterach* (Berthet 1981).

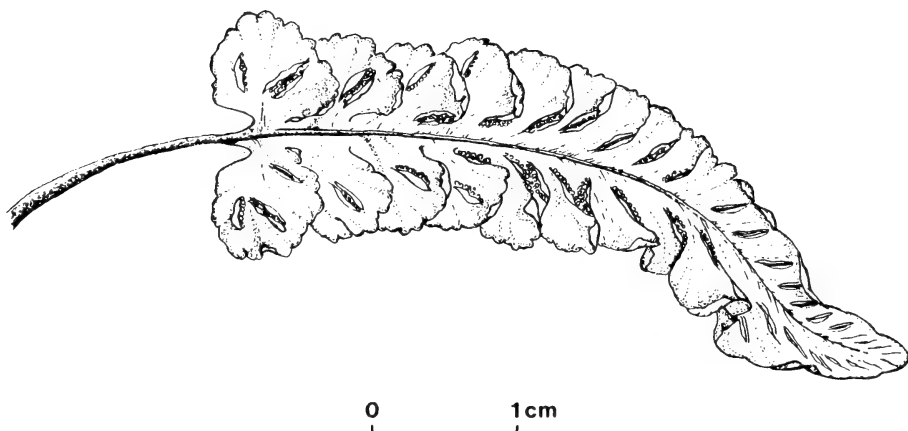
During field work in the Balearic Islands, in 1987, a plant was found in Mallorca whose morphology, ecology and cytology strongly suggest that we are dealing with a hybrid involving either *A. sagittatum* or *A. scolopendrium*, and *A. trichomanes*. The description of this

plant as a new hybrid named *A. × artanense* as well as a discussion on its proposed parents follow.

MATERIAL AND METHODS

Only one plant of this hybrid has been found in Mallorca, therefore a decision in order to keep it alive in the field was made. Only a limited number of fronds were cut to be pressed or fixed, and to serve as herbarium specimen. The description of the morphology is based on field notes and pressed fronds. Developing sporangia were fixed in the field, stained, squashed and preparations made permanent according to the method of Manton (1950).

FIGURE 1: Drawing of the lower side of a frond of *A. × artanense*.



MORPHOLOGY OF THE HYBRID

Fronds up to 6 cm × 1.5 cm, narrowly triangular with undulate margins (Fig. 1). Petiole about 1/3 as long as lamina, sparsely covered with scales. Lamina coriaceous, dark green in the upper side and light green in the lower side, with sparse scales; pinnatipartite for the lower 2/3 of its length, the upper third being entire. Basal pinnae almost orbicular, base cordate or cuneate, crenate. Middle pinnae broadly elliptic, crenate. Upper pinnae subrectangular, ill-defined (indistinct). Rachis brown in the lower half, green to the apex, with numerous scales. Sori divergent, 5-8 mm, single or in pairs. Sporangial content consisting of nearly misshapen spores of variable size (Figs. 2 A-D). Scales 0.4-1 mm, entire, subulate, dark brown without a central occluded area (Fig. 2 E).

This plant shows an intermediate morphology between *A. trichomanes* and either *A. sagittatum* or *A. scolopendrium* (Fig. 3). The texture of the lamina, the presence of some sori grouped in pairs, and the morphology and abundance of scales on the petiole, rachis and lamina indicate the influence either of *A. sagittatum* or *A. scolopendrium*. However, the outline of the lamina, slightly wider at the base than at the apex, suggests the influence of the cordate or hastate base of *A. sagittatum*. The degree of dissection of the lamina, the crenulate margin and the divergent sori show the characters of *A. trichomanes*.

FIGURE 2: Photomicrographs of spores and scales of *A. \times artanense*. A: Sporangial content with mainly misshapen spores; B: Detail of some shrunken and ill-developed spores; C and D: S.E.M. pictures of a spore and detail of perispore pattern; E: Rachis and petiole scales.

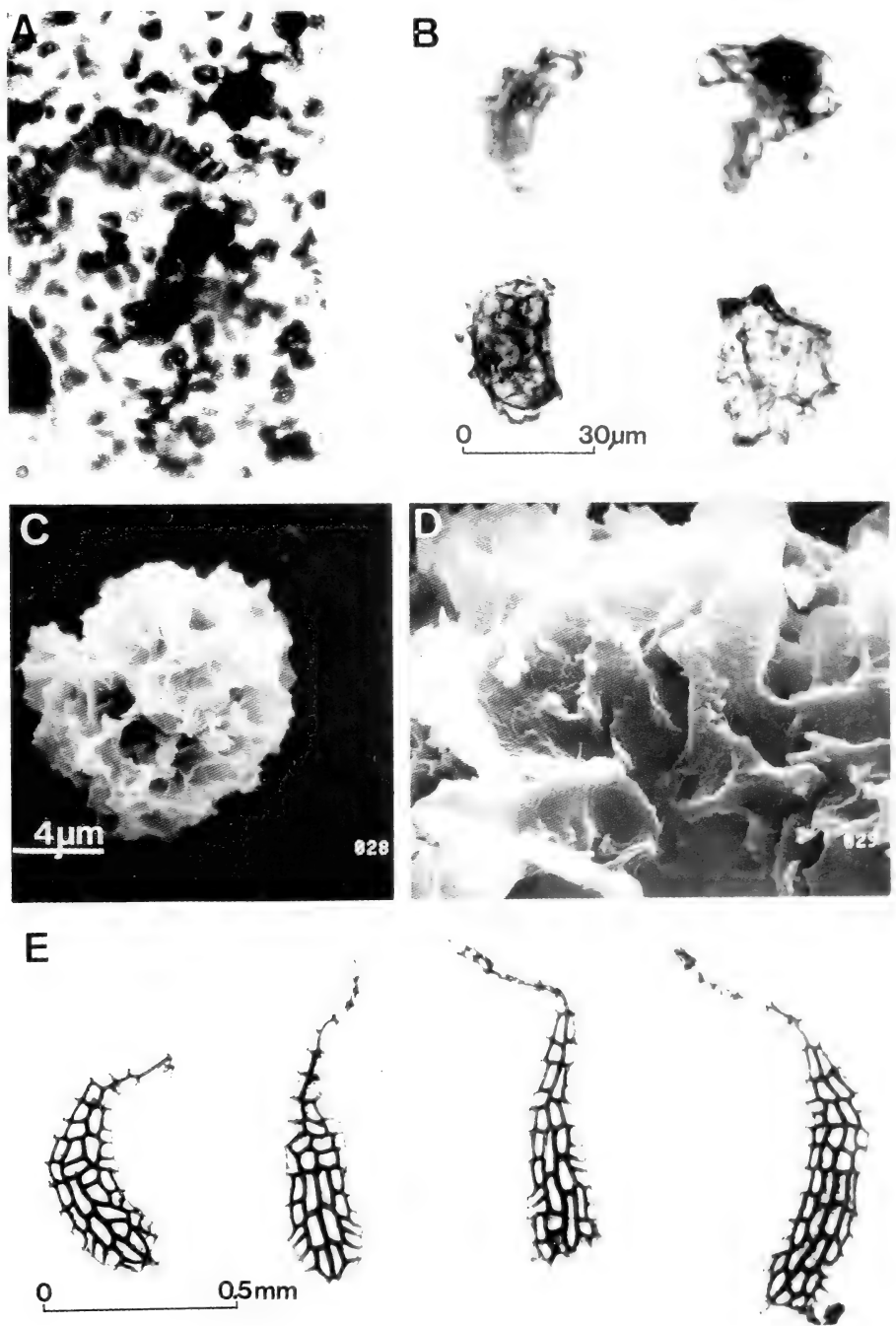
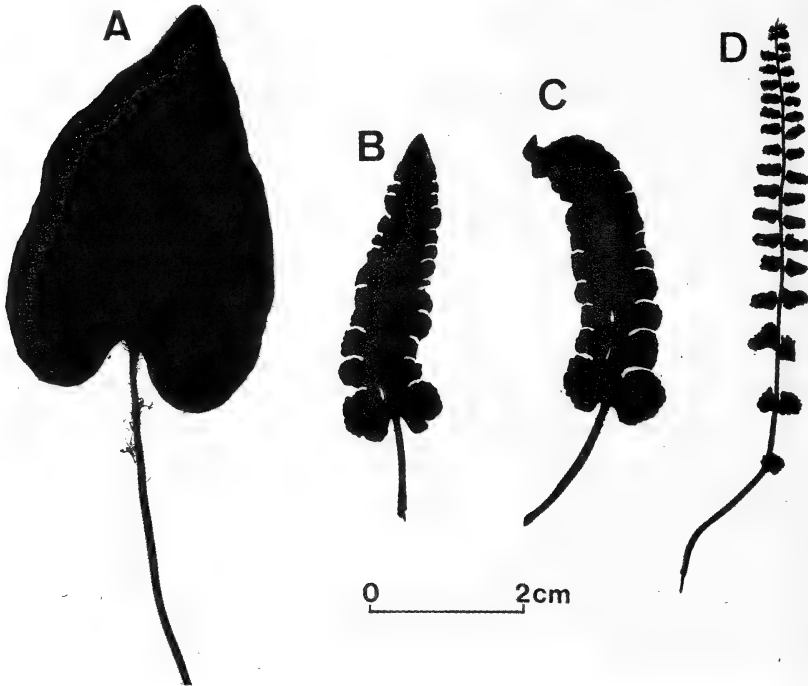


FIGURE 3: Silhouettes of *A. sagittatum* (A), *A. × artanense* (B and C), and *A. trichomanes* (D) from Artá, Puig d'En Xiroi.



CYTOLOGY OF THE HYBRID

This plant is a diploid hybrid showing an irregular meiosis (Fig. 4), with up to 72 unpaired chromosomes at metaphase I. In some cells 1 bivalent was seen, together with 70 univalents. Later stages of the meiosis are irregular resulting in the formation of nuclei of different size, and univalents lost in the cytoplasm. About half of the chromosomes are larger than the others. These results indicate that two different genomes, showing no synapctic homology in meiosis, are present in this plant.

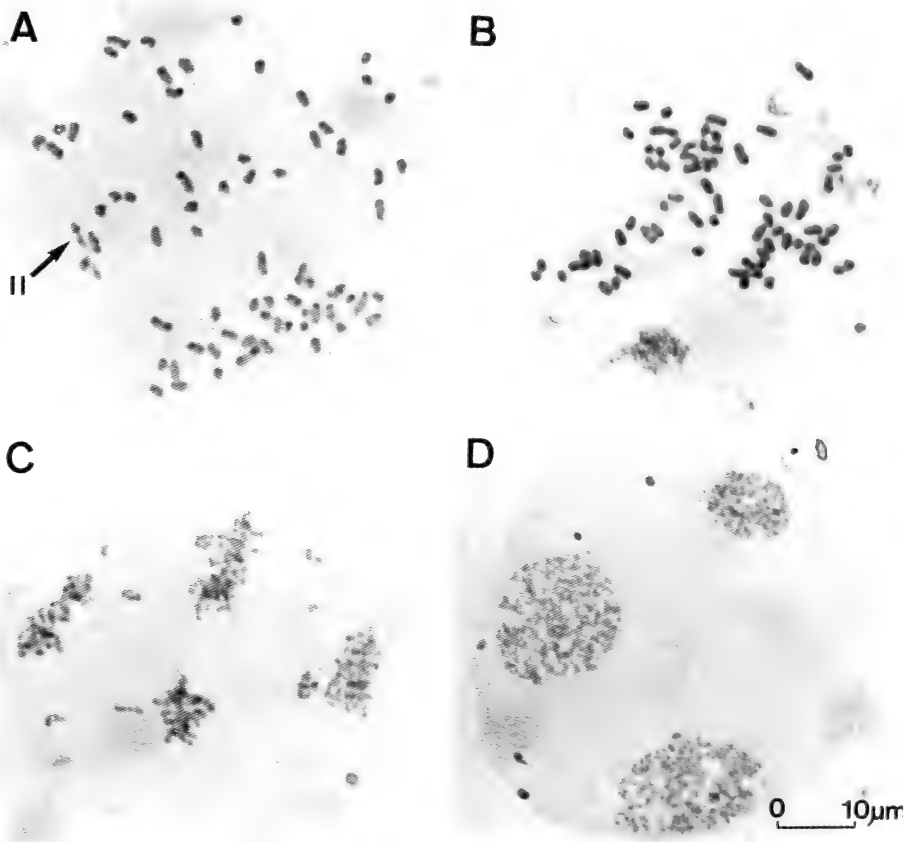
ECOLOGY OF THE HYBRID

The hybrid plant grows in a rock crevice, at the base of the NW-facing steep-walled outcrop of carbonate rocks. Other plants restricted to this type of environment were found in the vicinity: *Galium crespianum* J. Rodr., *Digitalis minor* L., *Micromeria filiformis* (Ait.) Benth., *Crepis triasii* (Camb.) Nyman, and *Sesleria insularis* Sommier. Several plants of *A. trichomanes* and *A. sagittatum* were also found in the immediate vicinity (Fig. 3).

DISCUSSION

This diploid hybrid must have originated from the cross of two diploid plants with no homology between their genomes. The morphology strongly supports that the hybrid is a cross between a diploid *A. trichomanes* with either *A. sagittatum* or *A. scolopendrium*. Besides, distinct differences in size of the individual chromosomes present in the hybrid support this hypothesis. Manton (1950) shows that *A. scolopendrium* presents larger chromosomes than other *Asplenium* species, a result confirmed in wild and synthetic hybrids involving *A. scolopendrium* as one parent (Girard & Lovis 1968; Lovis & Vida 1969; Vida

FIGURE 4: Cytology of *A. × artanense*. A: Metaphase I, $1^{II} + 70^I$; B: Metaphase I, 72^I ; C: Anaphase II with lagging chromosomes, some appear to be splitting; D: Telophase II, three nuclei of different size and a few chromosomes.



1970). *A. sagittatum* seems to have chromosomes of similar size to those of *A. scolopendrium* (Emmott 1964, Pl. 22-8).

Both *A. sagittatum* and *A. scolopendrium* grow in Mallorca, however, they are associated with different habitats in the island. *A. scolopendrium* grows either within vertical cavities in a mostly karstic landscape or within crevices in the narrow and steep-walled bounding sides of small streams (locally known as “torrents”). In both cases, shade and high humidity characterize the sites in which this plant grows. *A. sagittatum* endures drier and brighter conditions. In the Artá region (Eastern Hills) only *A. sagittatum* has been found and, in fact, is growing nearby the hybrid. Thus, the ecology of the hybrid site as well as the presence of *A. sagittatum* in the vicinity of the hybrid strongly suggest that *A. sagittatum* is one of the parents of the hybrid. Therefore, the large chromosomes observed in the meiosis of the hybrid must have been supplied by the *A. sagittatum* parent.

Concerning the other parent of the hybrid, another unrelated diploid taxon has to be chosen in order to explain the cytological behaviour of the plant. Again, the morphology and field spatial relationships between the hybrid and *A. trichomanes* plants, lead us to consider this taxon as the other parent of the hybrid. Following the taxonomy proposed for this aggregate species by Lovis (1964) and Lovis & Reichstein (1985), diploid plants

of *A. trichomanes* growing on calcareous rocks may be included in the subsp. *inexpectans*. However, it should be noted that some of the *A. trichomanes* plants growing in the Artá region, deviate from the morphology of subsp. *inexpectans*. These plants have small spores (mean exospore length ranging from 29.5 to 30.2 μm), thus indicating that they probably are diploid. However, they have narrow pinnae with serratolobate margins, a feature which recalls the morphology of the tetraploid subsp. *pachyrachis*, a taxon not found in Mallorca. Moreover, plants from other places of Mallorca, with similar morphology and mean exospore length, have been cytologically checked, and have proved to be diploids (e.g. samples from Mortitx, mean spore length = 27.27 μm , $n = 36$ bivalents).

Further research is in progress to elucidate whether: a) subsp. *inexpectans* is a highly polymorphic taxon, and therefore, in spite of their morphological variability, all the diploid plants growing in Mallorca can be ascribed to this subspecies, or b) another diploid taxon within the *A. trichomanes* complex (apart from subsp. *inexpectans* and subsp. *trichomanes*, and closely related to subsp. *pachyrachis*) should be considered, and deserve a formal taxonomic recognition.

Since this topic may remain as an open question for some time, we ascribe all the diploid *A. trichomanes* plants found on carbonate rocks in Mallorca to the subsp. *inexpectans* and so we propose that most probably a plant of this subspecies was involved in the origin of the hybrid plant.

CONCLUSION

Based on the above presented evidences, we conclude that the studied diploid hybrid has resulted from the cross of *A. sagittatum* and *A. trichomanes* subsp. *inexpectans*, and we propose to name this new hybrid as *A. \times artanense*, whose formal description follows:

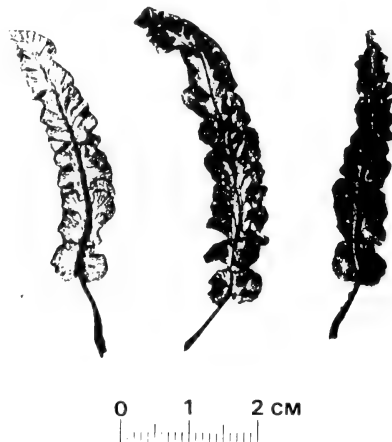
Asplenium \times artanense Rosselló, Cubas, Gradaille and Sastre, **hybr. nov.** (= *A. sagittatum* (DC.) Bange \times *A. trichomanes* L. subsp. *inexpectans* Lovis).

Diagnosis: Planta hybrida diploidea, media inter parentes. Frondes usque ad 6 cm longa et 1.5 cm lata. Fronde angustate triangulare, pinnatipartita, paleacea, basi auriculata. Sporae abortivae. Meiosi chromosomatibus univalentibus 70-72 et bivalentibus 0-1.

Holotypus (Fig. 5): Spain, Mallorca, Artá, Puig d'En Xiroi, 15.5.1989, 200 m alt., in a limestone crevice, J.L. Gradaille et al., MAF 131406, growing with *A. sagittatum* and *A. trichomanes* subsp. *inexpectans*.

Derivatio: Named after the town of Artá (Mallorca).

FIGURE 5: Fronds of *A. \times artanense* (holotypus).



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A NEW NATURAL HYBRID IN THE GENUS *PTERIS* (PTERIDACEAE: PTERIDOPHYTA) FROM THE KUMAUN HIMALAYA

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ABSTRACT

Pteris × *khullari* a new natural hybrid is described. One of the parents is presumably *Pteris wallichiana*. This is the only report of a natural hybrid of the genus *Pteris* from the W. Himalaya.

INTRODUCTION

In the recent past, natural hybrids have been widely assumed to be absent in the Himalaya, as the species were mostly not properly known. Hybrids can be detected by the presence of a high percentage of abortive spores, combined with an unusual morphology intermediate between the parents, and also irregular meiosis.

Till recently, only a single natural hybrid from the W. Himalaya was known (a diploid hybrid *Athyrium* × *pectinatum* Mehra & Bir 1960). Later Fraser-Jenkins (1986) added 5 more natural hybrids of the genus *Dryopteris* and 2 in the genus *Polystichum* (pers. common. to S.P. Khullar). Two natural hybrids in the genus *Cystopteris* were reported by Khullar (1983) from the Patnitop area (Kashmir). In addition to these, the common natural hybrid *Asplenium* × *alternifolium* was known from Kashmir (Stewart 1945, 1972), the latter also found in Kinnaur, Himachal Pradesh (Khullar & Sharma 1987).

THE DISCOVERY

During a survey of the ferns of the Kumaun Himalaya, an unusual taxon was collected from Pithoragarh district. On examination it was found to be a hybrid with a high percentage of abortive spores. This taxon belongs to the Section *Campteria* of the genus *Pteris*, as it possesses the typical costular areolae. To this section belong only 2 species in the W. Himalaya viz: *Pteris biaurita* L. (diploid apomictic and triploid apomictic Manton & Sledge 1954, Verma in Mehra 1961) and *Pteris wallichiana* Ag. (diploid sexual, Löve et al. 1977). One of the likely parents of the present taxon is *P. wallichiana*.

This taxon has been named after Dr S.P. Khullar, Botany Department, Panjab University, Chandigarh (India) in recognition of his contributions to the study of W. Himalaya ferns and also for detecting this hybrid in the fern collections of Kumaun sent to him for identifications.

DESCRIPTION

Pteris × *khullarii* Pangtey, Samant et Verma *hybrida nova*

Rhizoma erectum, apice squamis fuscis concoloris vestitum. Stipes c.30 cm longus, stramineus, crassus, 0.2 cm in diametro, glaber, nitidus. Rhachis stipiti similis, glabra. Lamina pinnata vel bipinnata, c.30 cm longa, 20 cm lata, triangulari-lanceolata, herbacea, glabra. Pinnae multijugatae, usque ad 15 cm longae, c.10 cm latae; pinnis basalibus maximis, alternatis, petiolatis, pinnulis bene evolutis instructis; pinnis distalioribus gradatim minus lobatis demum elobatis; omnibus pinnis margine varie lobatis in lobis anguste-linearibus integre aut lobate marginatis incis. Pinnulae multijugatae, c.4-6 cm longae et 0.25-0.3 cm latae, alternatae, breviter petiolatae, in



FIGURE 1: Diagrams of *Pteris x khullarii*

- a. part of the frond
- b. an ultimate lobe
- c. part of the frond to show venation
- d. various types of pinnules
- e. spores

parte distale pinnae sensim sessiles, margine integre aut varie lobatae, apice acutae, venis liberis, simplicibus, in lobis furcatae sed venis binatis basalibus acroscopicis basicopicisque anastomosantibus series areolarum costularum formantibusque. Sori marginales indusiati lobis varie fertilibus. Sporae fuscae, pro parte maxima abortivae.

Holotypus: W. Himalaya, Uttar Pradesh, Kumaun, Maupani, between Thal and Didihat about 0.5 km from Sandeo by the short route towards Thal, exposed place in the forest, c.2000 m alt., coll. Pangtey & Samant SPK 70.

Rhizome erect, apex scaly, scales brown, concolorous. Stipes c. 30 cm long, stramineous, thick, 0.2 cm dia., glabrous, glossy. Rhachis similar to stipe, glabrous. Lamina 1-2 pinnate, c. 30 cm long, 20 cm broad, triangular-lanceolate, herbaceous, glabrous. Pinnae many pairs, up to 15 cm long, c. 10 cm broad. Basal pinnae the largest,



FIGURE 2: Silhouette of *Pteris × khullarii*

alternate, petiolate. Pinnae in the distal region of the frond gradually less lobed and then lamina only once pinnate. Pinna margins variously lobed into narrow linear lobes with entire or lobed margins. Pinnules in many pairs, c. 4-6 cm long, 0.25-0.3 cm broad, alternate, shortly petiolate becoming sessile in the distal region of the pinna, linear, margin entire or variously lobed, apex acute. Veins free, simple, forked in the lobes, but the basal pair of acroscopic and basiscopic veins anastomosing to form a row of costular areolae. Sori marginal, indusiate, the lobes variously fertile. Spores brown, a large percentage of aborted spores present.

ACKNOWLEDGEMENTS

We are highly grateful to Prof K.U. Kramer (Zürich, Switzerland) for confirming the hybrid nature of the present taxon. We also wish to express our grateful thanks to Dr Paolo Luzzi (Curator, Botanical Gardens, Florence, Italy) for the Latin diagnosis.

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MODULAR GROWTH OF *HUPERZIA SELAGO* (LYCOPODIACEAE: PTERIDOPHYTA)

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ABSTRACT

Huperzia selago is an evergreen perennial of arctic and alpine environments. It demonstrates modular growth as it consists of a series of annually produced segments which can be aged.

H. selago demonstrates a very deterministic* pattern of growth with early dichotomous branching followed by infrequent branching as the lower parts of branches become decumbent. Relative growth rates are very low and characteristic of species of stressed environments in which it is found.

H. selago has a high vegetative reproductive capacity through the production of bulbils, which are readily established in relatively closed vegetation. The bulbils are more successful as a means of vegetative spread in extremely patchy environments than the stononiferous habit. This form of reproduction is opportunistic in relatively closed vegetation compared to sexual reproduction. The species relies on spore production for long distance transport and opportunistic establishment in early successional habitats generated by disturbance and erosion on the tops and steep slopes of mountains.

INTRODUCTION

The sporophyte of *Huperzia selago* (L.) Bernh. ex Schrank is a widespread perennial of the stressed environments of arctic and alpine areas. It shows an annual cycle in which sporophyll and microphyll production by the apical meristem alternate (Case 1943). As a consequence, all segments of the plant can be aged (Headley 1986). This means that the modular concept (Prevost 1978) can be used to describe the age-related growth, fecundity, death and survival of branches (Callaghan *et al* 1986a; 1986b; 1990).

The application of the modular concept to the growth and physiology of the closely related stoloniferous plant, *Lycopodium anontinum* L., has been used to describe its foraging habit and response to spatially patchy environments (Callaghan *et al* 1986a). Also it has been shown that this species has potentially indefinite growth (Callaghan *et al* 1990). However, *H. selago* is a decumbent perennial that reproduces vegetatively by bulbils and despite having potentially indefinite growth, it is a short-lived perennial with a very different growth and reproductive strategy from that of *L. annotinum*.

This paper described in detail the modular growth of *H. selago* growing in three contrasting environments, one a temperate upland oceanic site in Snowdonia, North Wales, another an alpine subarctic site in northern Sweden and a third high arctic site in Svalbard.

Sites

MATERIALS AND METHODS

Material was collected from three sites: one below Carnedd Dafydd in North Wales (53° 09' N, 3° 58' W.); one on Mount Njulla in the Abisko National Park in Swedish Lapland (68° 24' N, 18° 42' E.) and one on Svalbard (78° 15' N, 16° 30' E). The site in Snowdonia is an acid grassland at 580 m a.s.l. on a stabilised talus slope. The vegetation is dominated by *Nardus stricta* L. and *Festuca ovina* L. with *Vaccinium myrtillus* L., *Galium saxatile* L., *Anthoxanthum odoratum* L., *Cryptogramma crispa* (L.) R.Br. ex Hooker, *Campylopus paradoxus* Wils., *Hypnum cupressiforme* Hedw., *Polytrichum alpinum* Hedw.

*n.b. The terms *deterministic* and *opportunistic* are used in the sense of plasticity in growth and reproductive strategies of the plant, and not used in a morphogenetic sense.

and *Rhytidiadelphus loreus* (Hedw.) Warnst, also present. The site at Abisko is close to the summit of Mount Njulla (1160 m a.s.l.) which supports a dry mountain heath vegetation. This is dominated by *Salix herbacea* L. and *Cassiope tetragona* (L.) D. Don, with *Festuca ovina*, *Vaccinium vitis-idaea* L., *V. myrtillus*, *Salix polaris* Wg., *Silene acaulis* (L.) Jacq., *Carex bigelowii* Torr. ex Schwein. and *Polytrichum alpinum* also present in the vegetation (see Headley 1986 for further details). The site on Svalbard is on a south-facing snow-free ridge at 200-250 m a.s.l. and the vegetation is dominated by *Salix polaris*, *Cassiope tetragona*, *Polygonum viviparum* L. and *Carex rupestris* All.

Material

Branches of *H. selago* only grow apically and branch by true iso-dichotomy (Øllgaard 1979). Senescence proceeds distally with the microphylls and sporophylls remaining *in situ*. There is an annual alternation in the production of sporophylls and microphylls. Sporophylls are initiated at the beginning of the growing season and the apical meristem changes to initiating microphylls at the end of the growing season (Case 1943). The sporangia require over a year to mature, but they do not normally dehisce and release the spores until the winter after they have matured. Bulbils are generally initiated with the microphylls and are supported by specialised structures (bulbil bases) which persist like the microphylls. The bulbils and microphylls take a year to mature and bulbils are released in the autumn and winter following initiation (Case 1943). This pattern of growth means that annual segments of plant can be aged by counting back sequences of sporophylls and microphylls from an active meristem (Fig. 1).

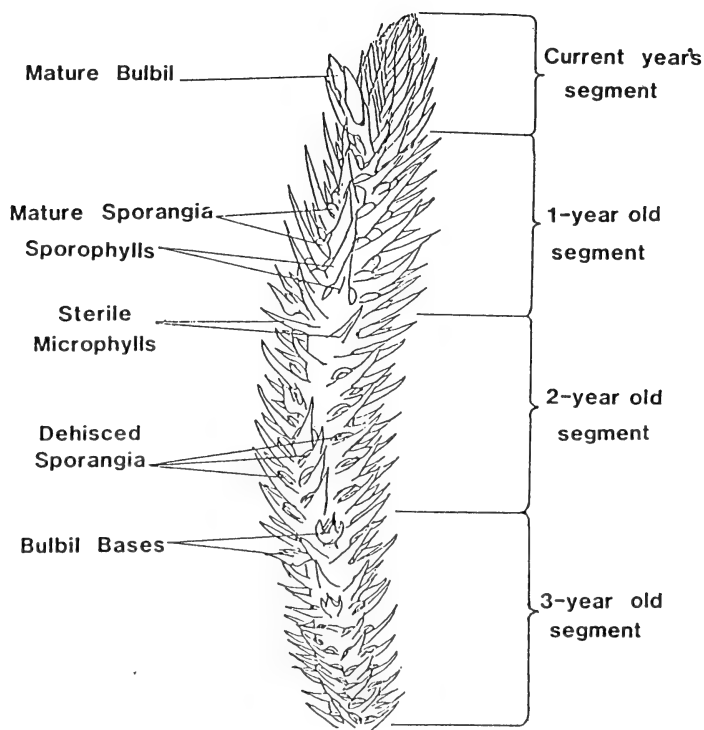


FIGURE 1. A branch of *Huperzia selago* showing four annual segments of growth.

Over the first 2 to 4 years of the life of a *H. selago* plant, bulbils and sporophylls are not produced. The segments of annual growth can still be identified however, by the slight reduction in the size of microphylls produced at the end of the growing season. The development of a plant of *H. selago* therefore enables the determination of overall plant age, as well as the ages of all segments, and the sequence of production of all segments within the plant (Fig. 2).

Roots are initiated just behind the apical meristem and grow down through the cortex (Saxelby 1908). They emerge from the base of the branches where they contact the soil and as a consequence they cannot be aged in contrast to the root system of *Lycopodium annotinum* (Headley *et al.* 1985).

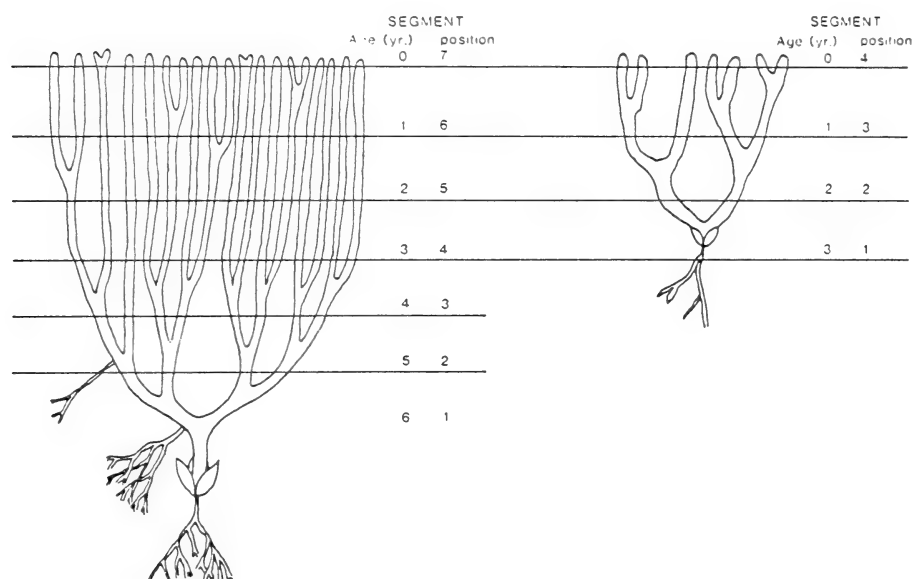


FIGURE 2. Schematic diagram of two typical *Huperzia selago* plants (one 7 years old and the other 4 years old) with the sequence of segment ages and segment position shown.

Methods

On 25th March 1982, 19 plants of *H. selago* were collected from the Snowdonia site and stored at -15°C until they were analysed. The plants were divided into their annual segments and classified according to their age and position (see Fig. 2). The number of bulbil bases on each segment was counted and the number of dichotomies was also recorded. The segments were dried at 105°C for 12 hours before being weighed individually. On 2nd August 1982, 18 plants of *H. selago* were collected from the Abisko site. They were dried and pressed before being analysed as above. Thirty seven plants were collected at random from Adventdalen, Svalbard in July 1987 and stored at -20°C prior to analysis.

A further 20 plants of *H. selago* were collected from the Snowdonia site complete with the soil in which they were rooted. The soil was carefully washed from their roots. The plants were aged and separated into roots and branches, before being dried and weighed. Ten fresh plants of *H. selago* were collected from the Snowdonia site on 10th October 1982 and the mature undehisced sporangia carefully removed and counted from each of 35 one year old segments. The one-year-old segments, spores and sporangial wall material

were dried and weighed as above. The number of spores per sporangia was estimated by suspending the spores dehisced from a known number of sporangia in 1 cm³ water containing a wetting agent and counting the number of spores in 0.1 mm³ of the suspension using a haemocytometer slide. Four separate counts were made for each of 3 separate suspensions, each containing the spores from 38 or more sporangia.

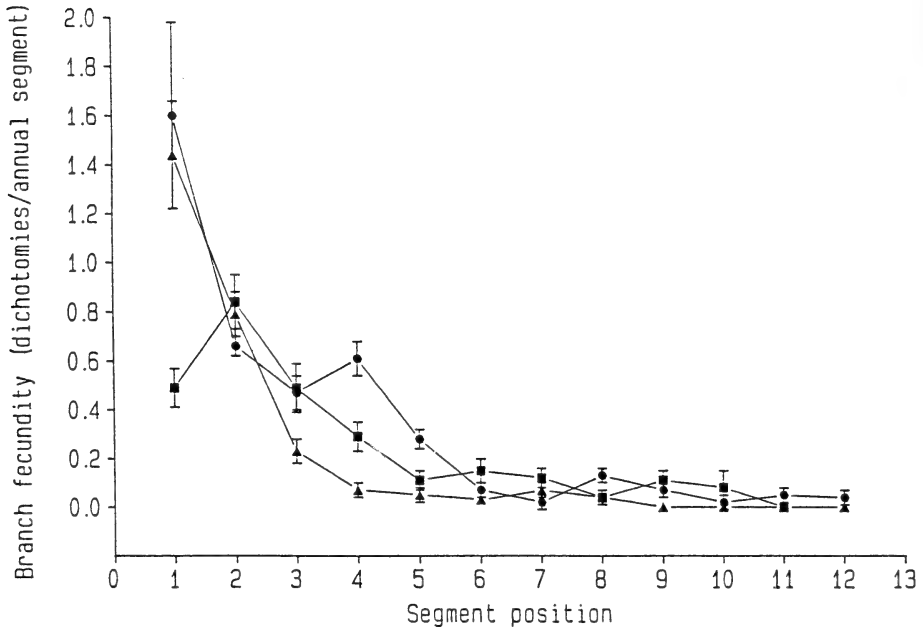


FIGURE 3. Changes in branch fecundity with increasing distance from the base of *Huperzia selago* plants, i.e. segment position, from Snowdonia (circles), Abisko (triangles) and Svalbard (squares). Means with S.E. bars shown.

The viability of spores from fresh branches was estimated by opening a fresh mature sporangium in a drop of lactophenol cotton blue (cytoplasmic stain) on a microscope slide. The numbers of stained and unstained spores were counted for transects across the slide until a total of 600 or more spores had been counted. This was repeated for a total of 9 sporangia.

RESULTS

Branch fecundity and mortality

The frequency of branching, or dichotomy, declines with increasing segment position, which is equivalent to increasing age of the whole plant, in all three populations. This results in the opposite of a tree-like structure (Fig. 3). There is a much lower frequency of branching in the Svalbard population in the first year. The Snowdonia population has a significantly higher dichotomy frequency than the Abisko and Svalbard populations in the fourth and fifth years. Overall the population which has much the lowest dichotomy frequency of the three populations is that from Abisko.

The mortality of branches is generally below 10% in the first five years of growth (Fig. 4). After this period mortality is generally highest in the Abisko population.

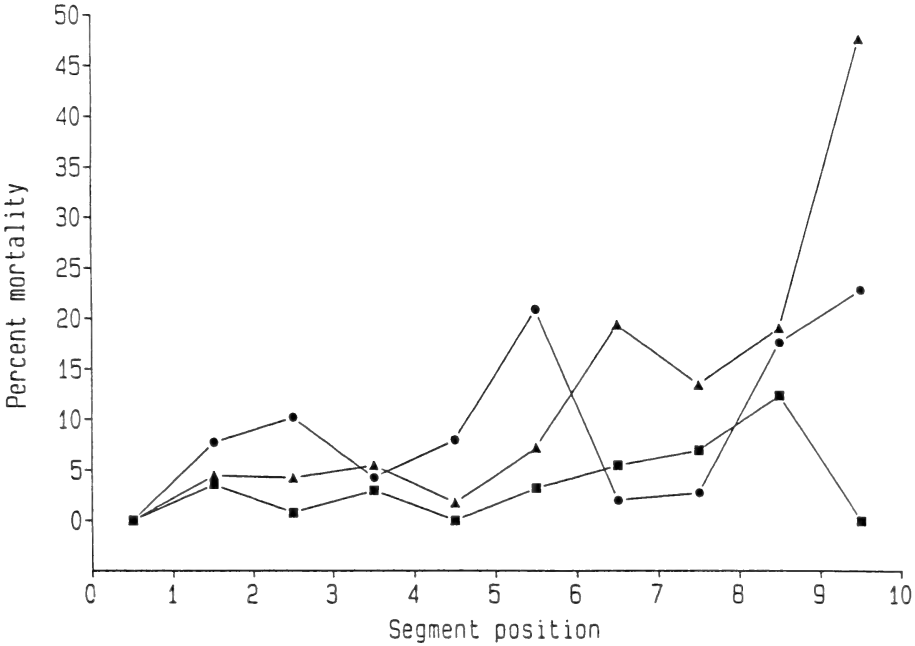


FIGURE 4. Changes in mean branch mortality (%) with increasing distance from the base of *Huperzia selago* plants from Snowdonia (circles), Abisko (triangles) and Svalbard (squares).

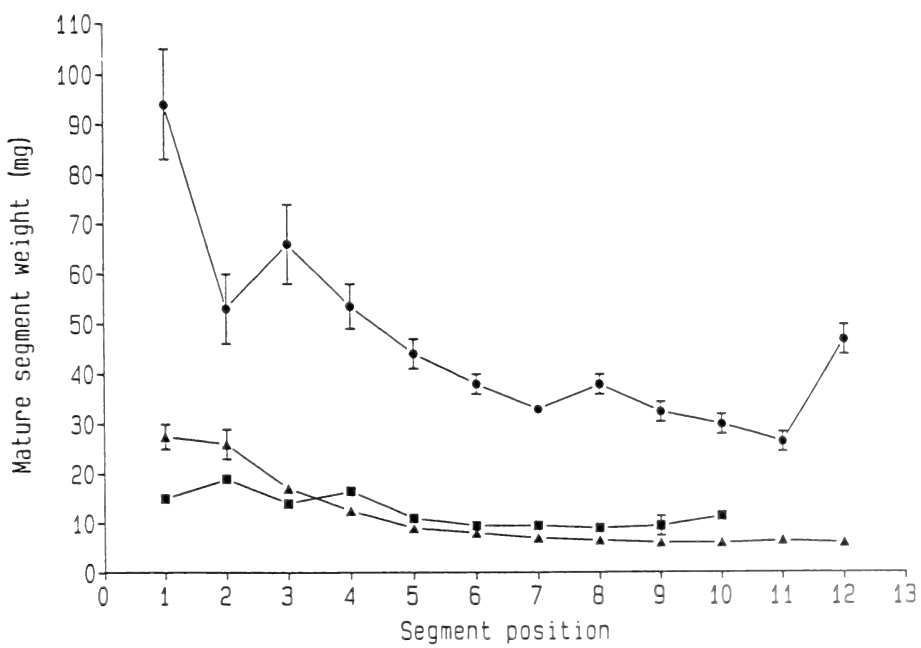


FIGURE 5. Changes in mature segment weight with increasing distance from the base of *Huperzia selago* plants from Snowdonia (circles), Abisko (triangles) and Svalbard (squares). Means with S.E. bars shown.

Growth of branches

The weight of segments is affected by a) the population they belong to, b) their position, c) their age and d) if they have dichotomised. Segments of material from Abisko weigh less than those from the other two sites (Fig. 5), while the segments of the Snowdonia population are by far the heaviest. In general, the basal segments are heavier than those higher up the plant (Fig. 5). As they age, dry weight is accumulated over one year in material from Snowdonia, whereas segments increase in dry weight over a 1-8 year period in material from Abisko and Svalbard (Fig. 6).

Larger segments are associated with dichotomies and segments with a dichotomy in material from Snowdonia were 72% heavier ($55 \text{ mg segment}^{-1}$) than those without ($32 \text{ mg segment}^{-1}$). There is however, an interaction between segment position, and age, and dichotomy which has not been quantified here.

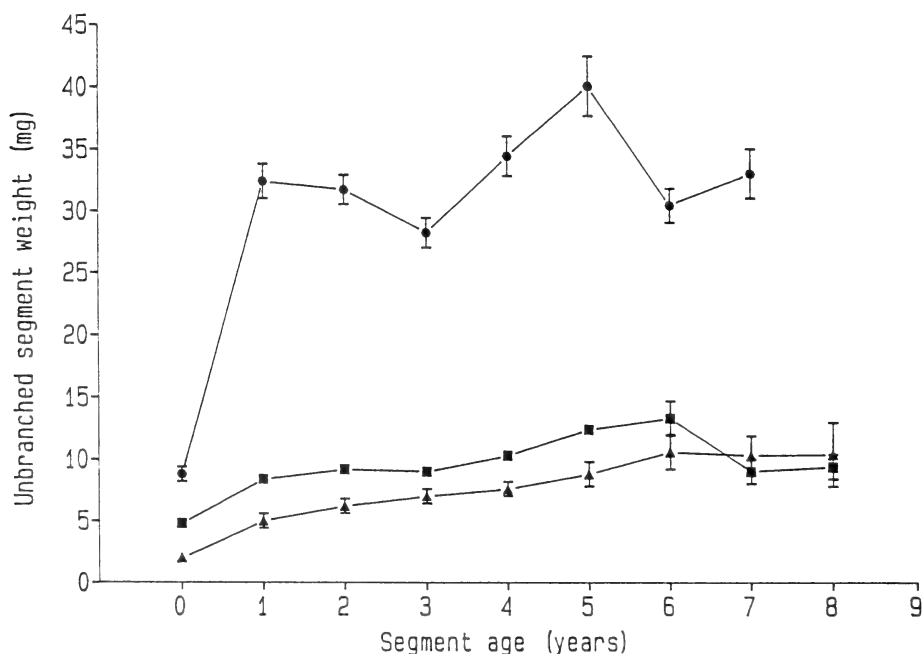


FIGURE 6. Changes in unbranched segment weight with increasing age in *Huperzia selago* plants from Snowdonia (circles), Abisko (triangles) and Svalbard (squares). Data is for segments of all positions. Means with S.E. bars shown.

Allocation of dry weight to roots

The proportion of total plant weight allocated to roots declines significantly from $24.6\% \pm 1.7\%$ in one year old plants to $9.8\% \pm 0.8\%$ in two or more year old plants from Snowdonia ($t=8.879$, d.f.=18, $p < 0.001$). There is no significant effect of plant age on the percentage biomass in the roots of 2 or more year old plants ($r=0.058$, d.f.=11, $p > 0.05$).

Total plant weight

There appears to be a biphasic growth pattern in total dry weight of plants for the Snowdonia and Svalbard populations (Fig. 6). The initially more rapid increase in dry weight (RGR

= 2.23 and 1.76 g g⁻¹ y⁻¹, calculated from data in Fig. 7, for the Snowdonia and Svalbard populations, respectively) is in the first two years of growth. The slower RGR after this is very low (0.375 and 0.136 g g⁻¹ y⁻¹). The total dry weight of the *H. selago* plants from Abisko showed no significant correlation with age.

Vegetative reproduction

As branches of *H. selago* grow apically, the basal segments become decumbent and as a result the plant spreads out either centrifugally on flat terrain or downhill on a slope. Fragmentation of a large plant in theory is possible, but large clones of *H. selago* are rare, with clones 1-2 metres across having only been reported from the undisturbed coniferous forests of Russia (Syelivanova-Gorodkova 1968).

The normal mode of reproduction is by bulbils, as all plants harvested or examined possessed the distinctively shaped leaves of the bulbil at the very base of the plant. The

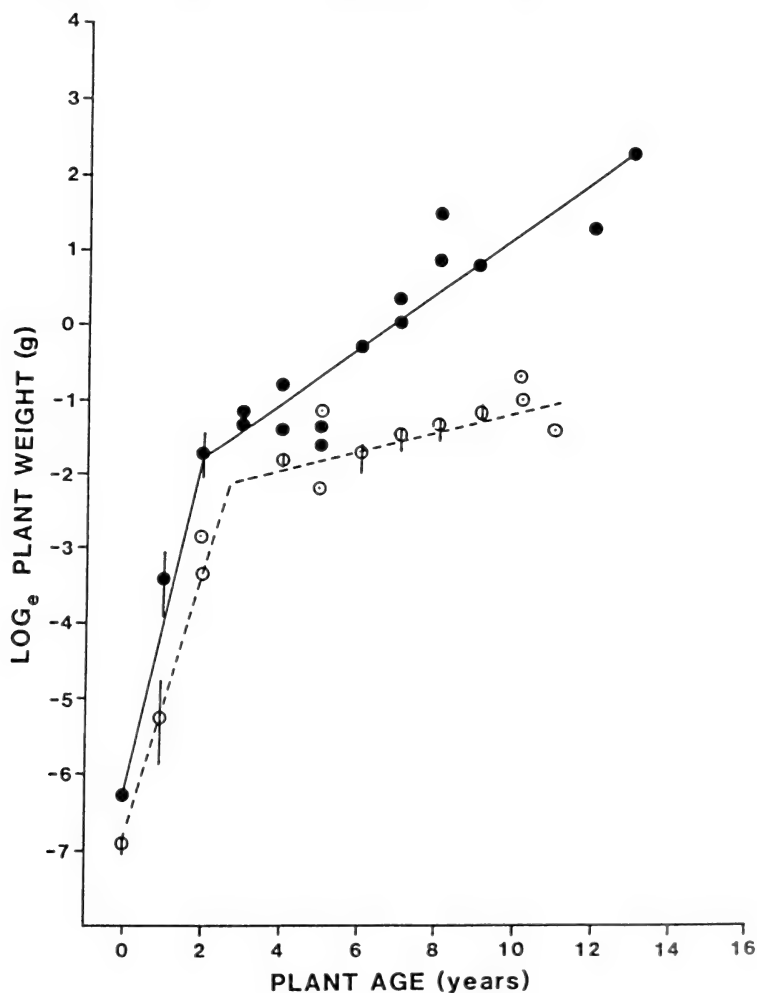


FIGURE 7. Relationship between whole plant weight (expressed on a logarithmic scale) and age of *Huperzia selago* plants from Snowdonia (solid circles and line) and Svalbard (open circles and dashed line). Means with S.E. bars shown for three or more replicates.

production of bulbils does not normally start until the third or fourth year of the plant's life (Fig. 8) and they are therefore, not released until the fourth or fifth year. The number of bulbils produced per segment increases with the age of the plant (Fig. 8). Despite the branch segments of the Abisko populations being lighter and hence smaller, the number of bulbils produced per segment is greater than that produced by the branch segments of the Snowdonia population over the first 8 years (Fig. 7). There is however, a much higher bulbil production per segment in the Snowdonia population later in the life of the plant (Fig. 8).

The mean weight of bulbils produced by the *H. selago* plants from Svalbard is intermediate (1.04 ± 0.06 mg) between those of the Abisko population (0.69 ± 0.04 mg) and the Snowdonia population (1.88 ± 0.10 mg).

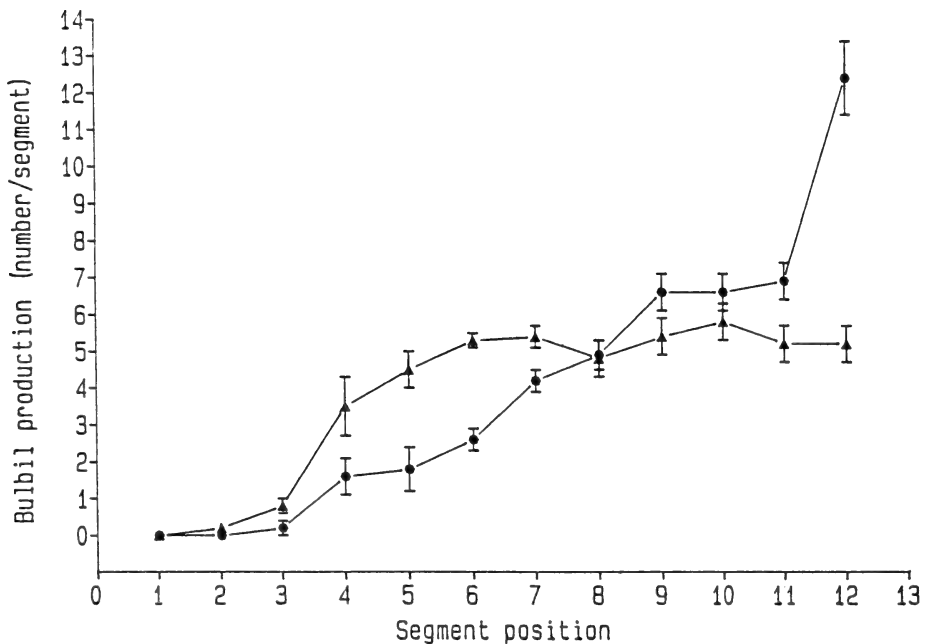


FIGURE 8. Changes in bulbil production with increasing distance from the base of *Huperzia selago* plants from Snowdonia (circles) and Abisko (triangles). Means with S.E. bars shown.

Spore production

Larger segments, which naturally weigh more, produce more sporangia (Fig. 9). The allocation to spores is $7.0\% \pm 1.2\%$ of the dry weight of the one-year-old segment which produces them. The number of spores in each sporangium is $19,000 \pm 2,000$. This means that a plant from Snowdonia, will produce on average 0.97×10^6 spores segment⁻¹. However the viability of spores is only $6.7\% \pm 2.2\%$.

DISCUSSION

H. selago is very widespread and frequently a component of montane, boreal and tundra environments, although it is never dominant in the communities in which it occurs (Headley 1986). It is a plant of very low relative growth rate and is consequently found growing in infertile habitats or niches within these environments (Headley 1986).

There is a very strong pattern of basal (positional) branching in *H. selago*, which does not differ very greatly between the populations sampled in this study or elsewhere (Turmel 1982). As *H. selago* does not have secondary thickening the basal branching which is the opposite to a tree-like structure, maximises the support of higher branches. However, the support is inefficient and individual branches gradually become decumbent at the base as the weight of a growing branch exceeds the capacity of the lower part of the stem to support it (Niklas & O'Rourke 1982). This pattern of basal branching is also observed in the vertical branch systems of the stoloniferous members of the *Lycopodiaceae*; *L. annotinum* and *L. clavatum* (Callaghan *et al* 1986a).

The annual weight increments of individual branches are generally very low, and are very similar to those of other evergreen tundra plants (4 to 62 mg y⁻¹) at Eagle Summit, Alaska (Miller 1982). The climatic conditions experienced on the top of Mount Njulla, are more severe than those in Snowdonia and mean segment weight is on average 77% \pm 3% lower in plants from Njulla compared to that of Snowdonia plants. Although climatic conditions affect segment weight, and age also affects the weight of developing segments, the position of the segment on the plant is the most important determinant of segment weight within any one plant.

H. selago differs from *L. annotinum* in not having a foraging strategy, but a tolerance of very stressed climatic and edaphic environments. *H. selago* is found as far north as Ellesmere Island and northern Greenland (82°N) and is found in soils that are naturally impoverished of major plant nutrients (0.4–18.2 ppm N; 4.4–5.8 ppm P). This is one reason for the very low RGR. The plant can respond to low phosphorus supply by increasing the rates of phosphate uptake (Headley 1986). However the plant can maintain much of its annual nutrient requirements by efficient internal recycling of the elements from basal segments to apical segments (50–80% for nitrogen and 40–60% for phosphorus) (Headley 1986). The immobility of *H. selago* compared to that of *L. annotinum* means that the plant has to be more efficient at capturing and utilising nutrients as root growth is restricted spatially. As a consequence, there is a much larger allocation of dry weight to roots in *H. selago* (10% of total plant weight) than in *L. annotinum* (5% of total plant weight).

Very old plants can become well established and have potentially indefinite growth in sheltered undisturbed forest habitats in Russia (Syelivanova-Gorodkova 1968). *H. selago* is however normally short lived (6–16 years) in the open habitats in Europe due to the premature death of the branches. As this species, like all the temperate members of the *Lycopodiaceae*, very rarely produces adventitious shoots, the removal of the branch tips by grazing or burning, as often happens in upland Britain, kills the plant. The plant may also show signs of premature death due to an inability to produce new roots as a consequence of being rooted in small crevices in rocks.

H. selago overcomes the problems of a limited life-span and immobility through successful reproduction by bulbils. *H. selago* plants may produce large quantities of bulbils over their whole life span, for example a plant from Snowdonia produced a total of 1166 bulbils over its 13 year growing period, which represented an investment of 18% of its dry weight to this form of reproduction. The allocation of this amount of dry weight to vegetative reproduction by bulbils is very similar to that observed for *Saxifraga cernua* and *Polygonum viviparum* (Wehrmeister & Bonde 1977; Petersen 1981). Reproduction by bulbils is particularly successful in the sparse vegetation of severely stressed and disturbed environments in the arctic (Bell & Bliss 1980; Callaghan & Emanuelsson 1985).

There is normally 100% germination of fresh bulbils which readily established on a wide range of substrata, including raw humus, peat, moss cushions, cracks in rocks, sand and rankers. This is typical for other species that reproduce by bulbils and plantlets (Harmer & Lee 1978b). This mode of reproduction is adequate for maintaining a viable population and spreading it within a particular site, especially a moderately closed community. The

large nutrient reserves within the bulbils (Smith 1920; Harmer & Lee 1978a; Headley 1986) are sufficient to enable the plant to grow up through competing grasses in the uplands of North Wales, the Lake District and Scotland, while opportunistic germination maximises the use of short growing seasons.

The distance between safe microsites are too great for *L. annotinum* to cross by means of subsidised growth of the stolon system in the extremely patchy environments of fell-fields, screes and mountain tops, and rhizomatous/stoloniferous plants cannot generally tolerate the disturbance associated with some of these habitats. It is here however, that *H. selago* and other bulbiferous/viviparous species have an advantage. The bulbils can successfully be transported by wind and water. This is a more opportunistic method of vegetation reproduction.

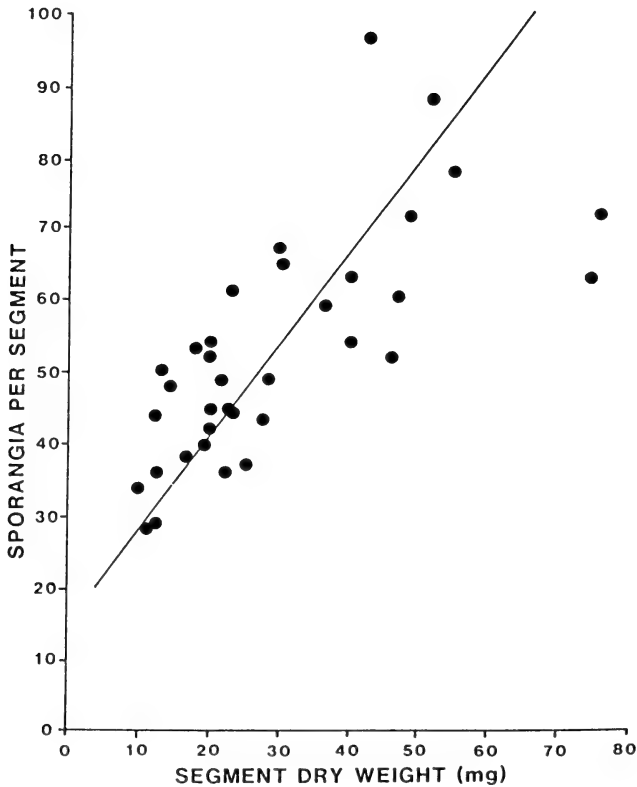


FIGURE 9. Relationship between the number of sporangia per segment and segment dry weight in *Huperzia selago* plants from Snowdonia. $r = 0.718$, $P = 0.001$.

The low allocation of dry weight to sexual reproduction (7.0%) and the absence of genets in closed vegetation is similar to that for *L. annotinum* and other perennials of the tundra (Chester & Shaver 1982; Callaghan & Emmanuëlsson 1985). *H. selago* can only successfully spread any significant distance by the numerous spores produced in the large sporangia. A single 13 year old plant, which had 248 spore bearing annual segments over its whole life will have produced approximately 2.4×10^8 spores. This also therefore, means that the probability of observing sexual reproduction (i.e. the gametophyte stage) is very low. For this reason and the fact that gametophytes of temperate *Lycopodium* species

(*sensu lato*) are generally subterranean, few collections of gametophytes, including *H. selago*, have been made. Those gametophytes which have been found, invariably occurred in open or disturbed habitats (Oinonen 1968; Bruce & Beitel 1979). Sexual reproduction is therefore more opportunistic than vegetative reproduction and has a similar function to that observed in *Viola* species (Newell 1983). The success of the widespread species *H. selago* in its stressed environment, depends therefore, on a balance between a strongly deterministic growth pattern and an opportunistic vegetative and sexual reproductive strategy.

ACKNOWLEDGEMENTS

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REVIEW

FLORA OF THE BRITISH ISLES by A.R. Clapham, T.G. Tutin and D.M. Moore. 1990, 3rd, and first paperback, edition. 688 pp. Cambridge University Press. ISBN 0-521-38974-7. Price: £25.00.

This is a welcomed book of a standard work, now at a reasonable price, and especially so because many of the more outrageous mistakes of the 1987 hardback 3rd edition have been corrected, e.g. *Asplenium cuneifolium* Viv. is no longer included as a British species. This work when originally written by Clapham, Tutin and Warburg (the latter was responsible for ferns) contained many gems of observation or opinion which, although often not substantiated, were stimulating. I notice that *Huperzia selago* spores are said to be 'non-functional', the plant reproducing by bulbils. I suspect this is not so and work carried out in North America by Joe Beitel suggests there is a complex of sexual species here and hybrids are common. There is an indication that European plants, including material from Britain, may also show some hybridity and contain more than one species. Notes are given on the morphology of the hybrid ferns in the British Isles which will be useful to many. Two nomenclatural corrections need to be made: unfortunate as it may seem to those that grow the pinnate-pinnatisect cultivar form of *Polypodium cambricum*, that name should be accepted for the plant we have hitherto called *P. australe* Fée. The plant that was originally called *Asplenium lanceolatum* Hudson and latterly *A. billotii* F.W. Schultz should now be called *A. obovatum* Viv. subsp. *lanceolatum* P. Silva.

For British botanists this Flora is now within grasp.

A.C. JERMY

**LYCOPODIELLA INUNDATA (LYCOPODIACEAE: PTERIDOPHYTA)
ON CHINA-CLAY AT LEE MOOR, S. DEVON***

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ABSTRACT

Records are presented from fieldwork in 1980-81 of density and distribution of *Lycopodiella inundata* in the disused south china-clay pit (SX 577593) at Smallhanger Down, Lee Moor, S. Devon, v-c- 3. There were about 3000 plants in three main habitats: humus-covered wet quartz sand, damp mounds of peat which are derived allochthonously from the surrounding moorland, and bare, saturated china-clay. It was in close proximity with *Drosera rotundifolia*, suggesting some association between the two species.

The substratum is nutrient poor, particularly in nitrogen (N) and phosphorus (P); as *D. rotundifolia* is insectivorous and obtains supplementary N and P supplies, the levels of these nutrients were analysed. The N content of *L. inundata* plants did not appear to vary with substratum, although the concentration of N increased slightly with an increase in humic matter. The N concentration in the substratum was correlated with the joint occurrence of *L. inundata* and *D. rotundifolia*.

INTRODUCTION

Following the report (Wigston *et al.* 1981) of *Lycopodiella inundata* (L.) Holub in abundance on old (1860-1955) china-clay working at Smallhanger, in 1980-81 visits were made to the site where an unusually high abundance of about 3000 plants of *L. inundata* in the south pit (SX 577593) and about 1500 in the north pit (SX 576595) were found growing in association with *Calluna vulgaris*, *Drosera rotundifolia*, *Juncus*, *Molinia caerulea*, *Potamogeton*, *Rhododendron ponticum*, *Rhynchospora alba*, *Salix atrocinerea*, *Scaprea*, *Sphagnum* and *Ulex gallii*.

L. inundata is a sub-Atlantic species, widely distributed throughout Western and Central Europe (Jalas & Suominen 1972), in Asia (Kuvaev & Rudskii 1973) and N. America (Hulten 1958). Its distribution in Britain shown by the *Atlas of ferns of the British Isles* (Jermy *et al.* 1978) indicates that its occurrence has declined since 1950, attributed (Jermy *et al.* 1978) to the drainage of acid wetland sites.

Despite its apparent decline in semi-natural sites there have been recent reports of it in man-made sites. Five plants have been recorded on quartz sand waste at Fox Tor Mires, S. Devon, v-c 3 (Wigston 1979), a maximum of seventeen plants at the base of a disused sand pit of Ling Common, W. Norfolk, v-c 28 (Petch 1980), and an estimate of at least 2000 plants at the base of a disused china-clay pit at Smallhanger, S. Devon (Wigston, Pickering & Jones 1981). This present study reports an investigation of the population of *L. inundata* at Smallhanger Down south clay pit, Lee Moor, S. Devon, v-c 3 (SX 577593).

THE HABITAT

Smallhanger south clay pit SX 577593 is situated on the south-west edge of the Lee Moor china-clay complex. The pit was worked in a small way from about 1860, until being abandoned in about 1955. The southern pit now has four quarry faces and one open side.

*Submitted to The Fern Gazette in December 1986. This unfortunate delay is regretted. EDITOR.

The faces have slopes of 30-60 degrees declining in slope towards the base. Erosion has caused a series of gullies and ridges which run perpendicular from some of the quarry faces.

The base of the pit is gently undulating, with substrata of acidic quartz sand and china-clay. The sand is free draining, but the fine china-clay is waterlogged where it has settled in hollows. The pit is at an altitude of 200 metres.

METHODS

An initial visual survey of the site showed that *L. inundata* grew abundantly in several vegetation types, but at different densities. An area was chosen for detailed investigation banded by four points: SX 57735929, 57785929, 57765925, 57735925 (Fig. 1).

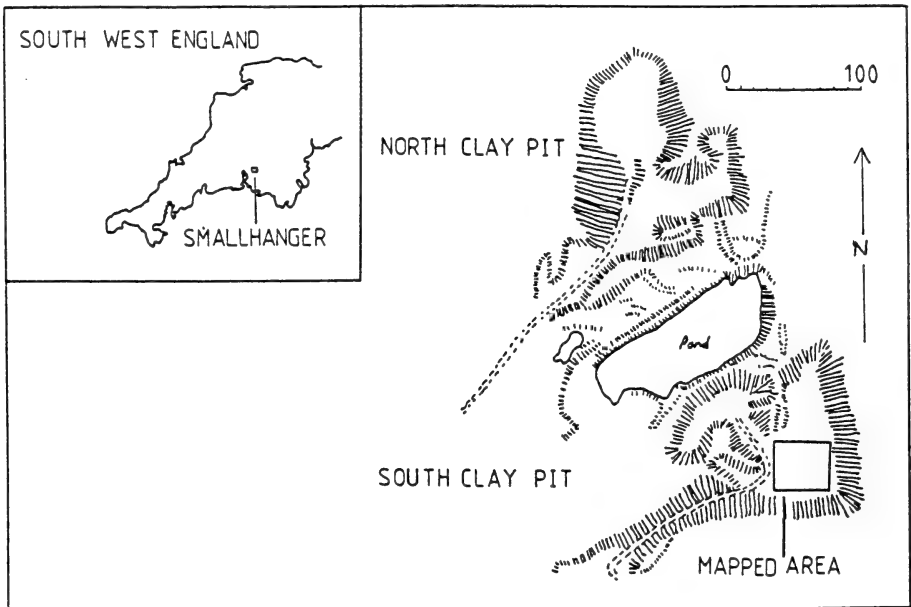


Figure 1. Smallhanger China Clay Pits (scale in metres).

This area included the main population of *L. inundata* in the clay pit, and also all the vegetation types delimited in the visual survey. Species lists were compiled for each vegetation type. Microtopographical and vegetation maps (Figs. 2 and 3) of the area were prepared using standard surveying techniques.

The survey established the boundaries of each vegetation type, contours at 25 cm intervals, and recorded each occurrence of *L. inundata* and *Drosera rotundifolia*. Quadrats were located in appropriate areas to record the density of *L. inundata* in each vegetation type in which it occurred within the mapped area. A 1m square quadrat divided by a wire grid into 10cm squares was used. For each quadrat details were drawn of every *L. inundata* plant, with an arrow used to indicate horizontal shoots and a dot to show vertical shoots. A typical quadrat is illustrated in Fig. 4.

VEGETATION TYPES

Twelve vegetation types were delimited (Fig. 3) in the initial survey:

- I A heath community dominated by *Calluna vulgaris*, with heath mosses and lichens, and some *Juncus*. There is much bare ground. This community was elevated slightly above the base of the pit, and the ground is damp, though not waterlogged,

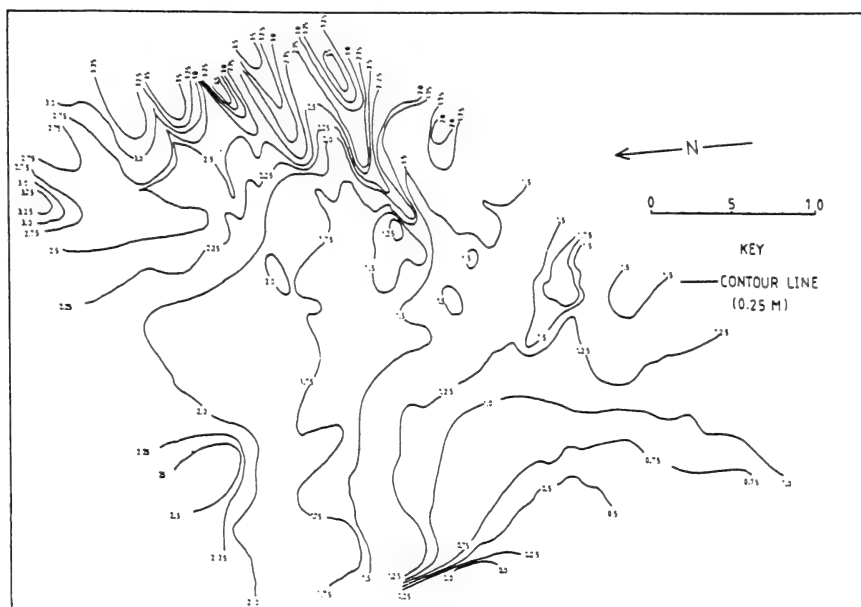


Figure 2. South Pit - microtopography (scale in metres).

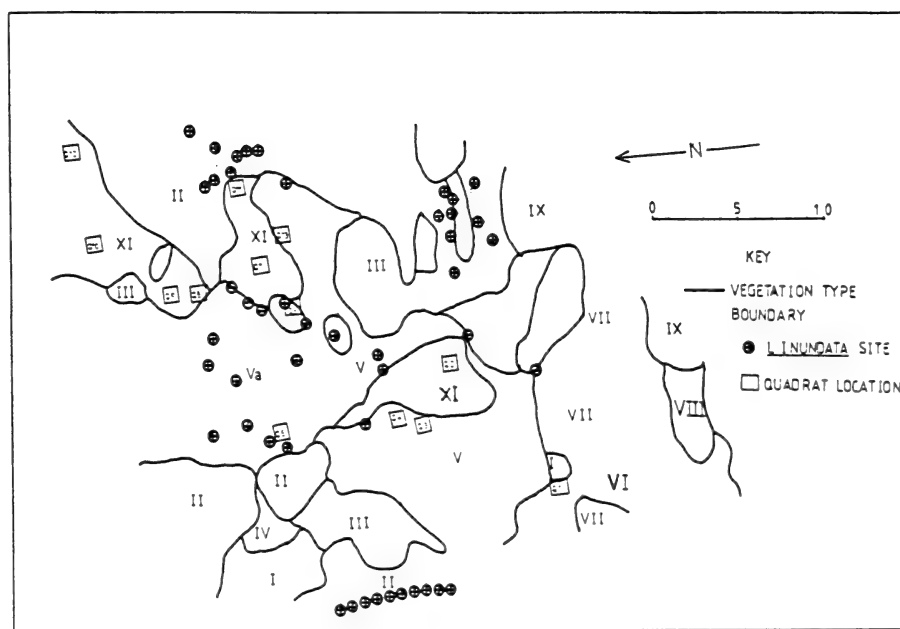


Figure 3. South Pit - vegetation types (scale in metres).

- II Elevated dry mounds, again dominated by heath species such as *C. vulgaris* and *Ulex gallii*, with *L. inundata* at the base of the mound,
III *Sphagnum* spp. with acidophile grasses and *D. rotundifolia*,
IV A damp hollow community with *Juncus* spp and *D. rotundifolia*,
V Waterlogged china-clay waste, with *Sphagnum* spp. and some *D. rotundifolia*,
Va The same as V but with *L. inundata* within *Rhynchospora alba*,
VI A *Sphagnum* dominated community, similar to III above, but without *D. rotundifolia*,
VII *Sphagnum* spp. with *Juncus* spp.,
VIII Open water with acidophile grass clumps,
IX Well drained quartz sand and gravel, with occasional mosses,
X *Sphagnum* spp., *Juncus* spp., and *Potamogeton* spp. growing on wet or waterlogged ground,
XI Vegetation dominated by *L. inundata* on slightly humic clay in association with *R. alba* and much *D. rotundifolia*; *Molinia caerulea* also present,
XII China-clay waste covered by open water (this may be a more waterlogged variant of V).

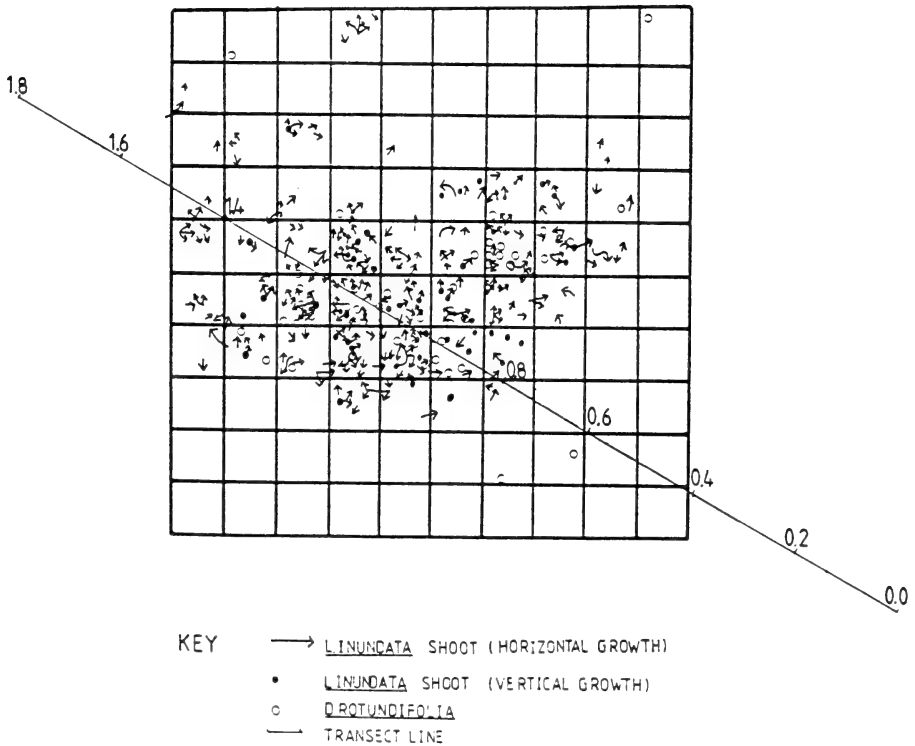


Figure 4. Quadrat 13 with transect line.

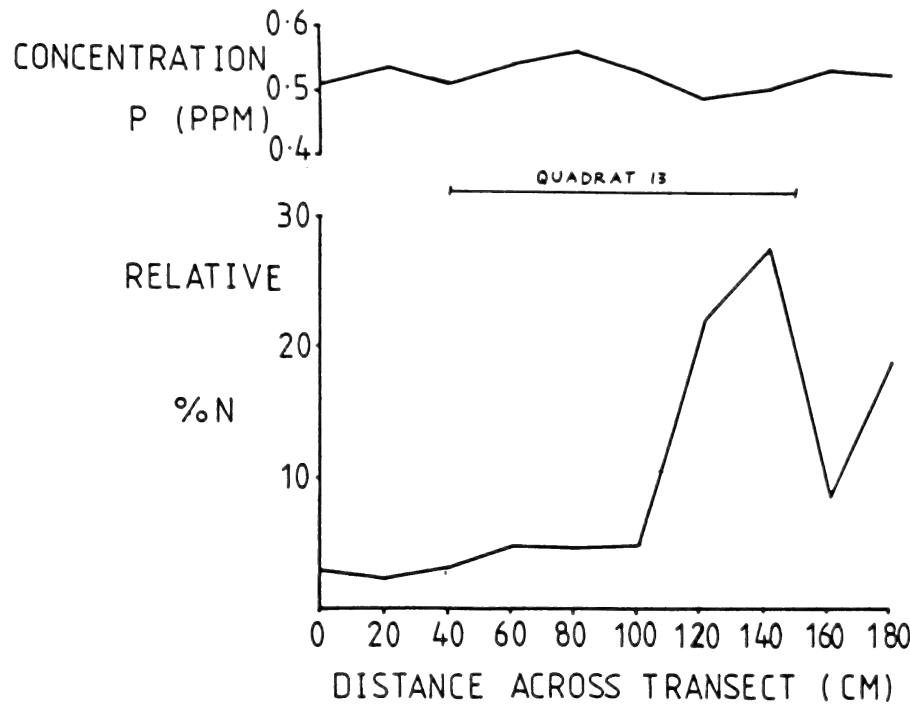


Figure 5. Transect across quadrat 13.

POPULATION ENUMERATION

The numbers of plants in each quadrat were counted (Tab. 1). One plant was counted for each vertical shoot and/or where one or more horizontal shoots appeared to originate. These numbers were converted to an average number of plants per quadrat of a particular vegetation type (Tab. 2). These density figures were multiplied by the number of estimated 1m² of *L. inundata* in that vegetation type to give the total number of plants of *L. inundata* in that vegetation type (Tab. 3). These totals were summed to produce the estimated total of 2979 plants, which is very large in comparison with other records in the South West (vice-counties 1, 2, 3). The importance of the china-clay habitat was increased by the discovery in March 1981 of a population of 1500+ plants in Smallhanger north clay pit, SX 57635953.

TABLE 1
Number of *L. inundata* plants in each quadrat

Quadrat number	Vegetation type	Number of <i>L. inundata</i> plants in quadrat
1	II	6
2	XI	290
3	XI	220
4	Va	4
5	Va	24
6	Va	121
7	XI	94
11	XI	68
13	XI	118

L. inundata did occur in quadrats 8, 9, 10 & 12, but an accurate count was not undertaken due to time limitations and an already abundant amount of population data for this vegetation type (XI).

TABLE 2
Average number of *L. inundata* plants per quadrat in each vegetation type

Vegetation type	Number of quadrats with <i>L. inundata</i>	Total number of <i>L. inundata</i> plants	Average number of <i>L. inundata</i> per quadrat
II	1	6	6
Va	3	149	49.6
XI	5	790	158

TABLE 3
Total population of *L. inundata* in mapped area

Vegetation type	Average number of <i>L. inundata</i> in vegetation type	Number of areas of <i>L. inundata</i> in that veg. type	Total number of <i>L. inundata</i> plants in that veg. type
II	6	25	150
Va	49.6	22	1091
XI	158	11	1738
Estimated total number of <i>L. inundata</i> plants in mapped area			2979

DISTRIBUTION

The southern Smallhanger pit contained three habitats in which *L. inundata* grew. These were:

- waterlogged china-clay waste with *L. inundata* within *R. alba* (vegetation type Va),
- L. inundata* growing on damp humus-covered china-clay with *R. alba*, *D. rotundifolia* and *M. caerulea* (vegetation type XI),
- elevated drier peaty moulds with *L. inundata* growing near the base (vegetation type II).

The vegetation boundaries were not always distinct; for example types Va - XI - II tended to occur in a transition from bare china-clay to peat substratum, and from waterlogged to damp, occasionally flooded, ground. Such transitions mean that vegetation types recorded in Fig. 3 are a general guide; specific local vegetation types are assigned for each quadrat (Tab. 1).

At Smallhanger, *L. inundata* will grow on a range of habitats, although it is apparent from its density figures (Tab. 2) that the favoured habitat is vegetation type XI, with an average of 158 plants per quadrat. Secondary habitats are vegetation type Va and II with an average of 50 and 6 plants per quadrat respectively. At Smallhanger the optimum habitat of *L. inundata* is a damp humus-covered clay waste, in association with *D. rotundifolia*. This finding is similar to that reached by Brunerye (1971) following work at Correze, France, he concluded that the optimum ecological conditions for the growth of the species was saturated peaty sands, with some gravel; he also concluded that sub-optimum habitats were:

- On the edge of peaty moors, in particular on the steep sides of hollows with peaty bottoms. The soil was mainly peat, but not as wet as the bottom of the hollows, which are normally saturated,
- When peaty sands are progressively covered with silt or mud; under these conditions *L. inundata* can only survive if it is regularly flooded, and as long as the density of other vegetation is not too great,
- On wet sand paths, where *L. inundata* was found to establish itself with *Juncetum silvatici*.

It seems that Brunerye's sub-optimum habitat (i) is analogous to the Smallhanger vegetation type II, and sub-optimum habitat (ii) to vegetation type Va.

The *Atlas of ferns of the British Isles* (Jermy *et al.* 1978) indicates that *L. inundata* currently occurs at few sites and at low population densities. Our work, and that of Brunerye (1971) suggests that the decline of *L. inundata* is not so much due to the drainage of acid wetland sites (Jermy *et al.* 1978) with a peat or bog soil (as this may only be a secondary habitat), but due to the rarity of the optimum habitat. Where wet humus-covered clay waste has occurred at Smallhanger it is able to flourish, particularly in association with *D. rotundifolia*.

NITROGEN (N) AND PHOSPHORUS (P) LEVELS

Work by Bradshaw *et al.* (1975) has shown that the nutrient levels in sand and mica waste are very low. The low levels of the most limiting nutrients, N and P, prevent the growth of many species on china-clay waste. Stone & Thorp (1971) investigated the growth of four species of the genus *Lycopodium* growing in circular clumps; they found that readily soluble N increased sharply at the point where the rhizoids first developed along the advancing *Lycopod* rhizomes.

To investigate the possible relationship between the growth of *L. inundata*, *D. rotundifolia* and the nutrient levels in the clay substratum at Smallhanger south pit, the total N concentration and available P of the soil was determined across a transect, traversing a circle of *L. inundata* growth. The transect analysed was located across quadrat 13 (Fig. 4) and crossed a circular growth of *L. inundata*, associated with *D. rotundifolia* on humus-covered china-clay, vegetation type XI. The ring of *L. inundata* was surrounded by bare china-clay, vegetation type XII.

A 1.8m transect line was laid across the area, and substratum samples were taken at 20 cm intervals. Field analysis of the substratum indicated a pH range of 4.2 - 4.7, the reading of lower pH occurring within the humus-covered china-clay, and the higher pH reading from the bare clay. The collected samples were dried and digested by the Kjeldahl technique (Brookes 1976); following digestion the solutions were diluted with deionised water, then analysed for N and P concentrations using a Technicon automatic-analyser. The results (Fig. 5) from this instrument gave *relative (not absolute)* N levels (due to the acid nature of the digest) and quantitative P levels. The N is illustrated according to the % N recorded rather than actual concentrations. The concentration of N in the substratum across the transect is shown to be low in areas of bare clay, but increased across the area of *L. inundata* growing on humus-covered clay waste in association of *D. rotundifolia*. In contrast the concentration of P in the substratum across the transect fell very slightly across the area containing *L. inundata*.

DISCUSSION

The marked increase in the concentration of N in the substratum across the transect is unlikely to be caused by the deposition of animal faeces, because there is no corresponding increase in the P concentration. It is possible that the lowering of soil P concentration across the area is due to its uptake by the vegetation. The large increase in the soil N concentration across the area with *L. inundata* may be due to either an input of N from *D. rotundifolia*, or to mycorrhiza on the subterranean part of *L. inundata*, or a combination of both. Further work needs to be undertaken to establish if there is any casual relationship between the occurrence of *L. inundata* and *D. rotundifolia*.

CONCLUSION

The Smallhanger south clay pit has a population of ± 3000 plants of *L. inundata*. This population occurs over three habitats: the optimum was humus-covered clay waste subject to flooding, and the sub-optimum were waterlogged china-clay and damp peat mounds.

Perhaps the main reason for the rarity of the species now in the British Isles is due to the scarcity of its optimum habitat, rather than a reduction in its secondary habitats due to drainage.

The increase of N concentration in the soil along the transect suggests that *L. inundata* has the ability to either produce or exploit reserves of N which gives it an advantage over other plants to grow abundantly in a normally nutrient-poor inhospitable habitat. However, growth with its associated vegetation undoubtedly improves the soil by increasing the available N enabling other species to invade the habitat. At Smallhanger there is currently a gradual invasion of herbaceous, shrub and tree species in the base of the pit (Wigston *et al.* 1981). *L. inundata* appears to act as a pioneer species of inorganic acid wetland.

ACKNOWLEDGMENTS

We would like to thank Mr Roger Davies, who first drew our attention to the site; English China Clay Lovering Pochin and Co. Ltd for permission to use the site, and particularly Mr J.V. Silverlock who supplied the history of the site; Susan Jones who gave invaluable help with fieldwork; and Chris Preston of the BRC, Monks Wood who supplied records of *L. inundata* in Vice-Counties 1, 2 and 3.

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THE UPTAKE AND TRANSLOCATION OF CAESIUM 134 AND STRONTIUM 85 IN BRACKEN *PTERIDIUM AQUILINUM* (DENNSTAEDTIACEAE: PTERIDOPHYTA)†

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ABSTRACT

This is a report of preliminary research in which the study of the morphology and physiology of bracken (*Pteridium aquilinum*) is combined with the investigation of uptake of radionuclides from accidental nuclear release. Monitoring the uptake and translocation of artificially applied radioactive caesium and radioactive strontium in bracken plants should help to indicate how these radionuclides with contrasting behaviour enter and cycle through a long lived element of an important ecosystem.

THE CHERNOBYL INCIDENT

The highest yield nuclear accident to date, on 26th April 1986 at a nuclear power station at Chernobyl, near Kiev, Russia, resulted in widespread contamination of the northern hemisphere. Caesium (Cs) 137 (radioactive half life 29.7 years) and 134 (radioactive half life 2.1 years), released in the ratio 2:1, were the most important radionuclides released, together with some strontium (Sr) 90 (half life 28 years). Radionuclide deposition was greatest in areas of high rainfall (Allen 1986).

INTERCEPTION AND RETENTION OF RADIONUCLIDES BY VEGETATION AND SOILS

Models had predicted that radioactive caesium would rapidly become unavailable to plants because it would bind to clay minerals in the soil. However, these models were based on lowland agricultural systems where soils are predominantly mineral (Howard & Livens 1987). The British areas most affected by Chernobyl deposition were permanent pastures on *organic* soils, which had 2-4 times higher Cs134 and 137 activity than improved pastures in the same areas. These areas are also areas of abundant growth of bracken *Pteridium aquilinum* (L) Kuhn. The high organic to low clay content of these soils ensured that the Cs 134 and 137 remained mobile (Howard & Livens 1987; Barber 1964) and available for transfer along the food chain ultimately to man. This will pertain for the foreseeable future, possibly for the entire half life of Cs137, because Chernobyl caesium is moving down the soil profile very slowly (Eggleton & Sandalls 1988).

The large surface area offered by bracken both above and below ground may intercept and then cycle radionuclides through these organic soils. Cs is cited by some workers as being an analogue of potassium (K) (Rickard 1966). As K is accumulated in the meristems of bracken it may be expected that Cs may be also concentrated there. Its long half life means that this could lead to genetic damage in the plant. Sr is known to be a good analogue of Ca. Sr85 may be found concentrated in the older parts of the plant like Ca (Russell 1963). An experiment over two seasons should show the long term seasonal translocation patterns of the two radionuclides. This will also help to illustrate nutrient allocation in this clonal plant. A short term experiment will contrast short term translocation patterns at different times of the year.

†One of the contributions to the BPS Autumn Indoor Meeting on 14 October 1989 at Whitelands College, London (see Bulletin 3 number 6), based on a poster entitled 'Radionuclide uptake, transport and effect on bracken' presented at the international conference 'Bracken 89', University of Sydney, 18-21 July 1989.

MOVEMENT OF RADIOACTIVE CAESIUM IN BRACKEN PLANTS

Two pilot experiments using Cs134 alone have been completed to develop the best method. In the first experiment mature roots, the rhizome shoot tip and pinna tip of 3 plants grown in perlite were immersed in 7,400 Bq/ml Cs134 in distilled water. 20 µl droplets of distilled water containing 185,000 Bq/ml Cs134 were applied to the frond of another plant. After 24 hours the samples were washed for 15 minutes to remove radionuclide from the apoplast.

The fronds were subjected to autoradiography. The rhizomes were cut up into their component parts i.e. rhizome shoots, frond primordia, rhizome pieces etc., fixed, and then counted for gamma emissions on a sodium iodide detector. The parts giving sufficient counts were then sectioned and subjected to microautoradiography.

Evidence of translocation (mainly in the phloem) was indicated when the radionuclide was applied to the rhizome shoot but not to anywhere else. If further experiments confirm this, an important nutrient uptake role for the rhizome tip is indicated by this. The second smaller experiment involved a plant being left for 7 weeks *in situ* after removal of the radionuclide solution from the root. Widespread translocation of the radionuclide was observed.

DISTRIBUTION OF STABLE CAESIUM AND STRONTIUM IN BRACKEN TISSUES

An analysis of stable caesium and strontium in different parts of plants should indicate where radioactive Cs and Sr will accumulate in bracken. Rubidium (Rb) and potassium are alkali metals like Cs so should similarly indicate its distribution. The analysis of K and calcium (Ca) also offers a way of comparing how these major plant nutrients are distributed relative to Cs and Sr. Samples have been taken from:- fronds, frond primordia, shoot tips, rhizome, roots and soil, with pure sucrose as a control. Cs and Rb were analysed by neutron activation and gamma spectrometry. Ca, Sr and K were measured by atomic emission spectrometry.

Results for 4 mature plants show that levels of the elements vary between sites and between tissues of the same plant. Rb and K appear to be preferentially accumulated in the rhizome meristem and frond primordia. However, Cs is not accumulated in any specific part of the plant. Ca and to a lesser extent Sr were concentrated in the senescing fronds. The concentration factors (quantitative expressions of the amount of element transferred from soil to plant parts) for 19 plants show Ca and Sr transfer from the soil to the senescent fronds is much greater than for any other plant part.

Ca is preferentially accumulated in the senescent fronds because it is a component of cell walls as calcium pectate. It also takes part in the control mechanism for growth and developmental processes and therefore is more abundant in active tissues like the frond rather than inactive tissues such as the rhizome; being immobile it concentrates in old woody tissue as more mobile elements are moved out. Sr acts similarly due to its analogy. Where photosynthetic fronds are present there were similar amounts of Sr and Ca to senescent fronds. Radioactive Sr therefore would be expected to be found in the leaf litter from where recycling to plants could take place. Although no firm conclusions can be drawn from the data for Cs, it appears that no analogy to K seems to exist for bracken. More data from neutron activation analysis should help clarify this.

THE POTENTIAL ROLE OF MYCORRHIZAS IN RADIOACTIVE UPTAKE

Mycorrhizas are known to increase the uptake of certain nutrients by plants. It may be possible to link greater uptake of Cs134 and Sr85 with the presence of mycorrhizas. Percentage infection was estimated (after Jones & Sheffield 1988) for random samples of roots from all the plants sampled. A correlation analysis was carried out between the amount of mycorrhizal infection and Sr, Ca and K contents in the plants and soil. No correlation was found. A similar investigation will be carried out for Rb and Cs.

THE POTENTIAL EFFECT OF ACID RAIN ON RADIONUCLIDE UPTAKE

The influence of acid rain on cuticle thickness and hence efficiency of radionuclide uptake is being investigated. If there is a cline in the thickness of the frond cuticle on plants taken from a transect between a "clean" and polluted area a radionuclide uptake experiment is planned.

CONCLUSIONS

This is preliminary research leading to short and long term experiments. The results from the pilot radionuclide application experiment show that Cs134 may be translocated in the phloem, but the stable element analysis indicates that it may not be preferentially accumulated in rhizome meristems. The latter may mean that the genetic material of bracken may not be damaged in the event of a nuclear accident. A previously unknown uptake role may be indicated for the rhizome shoot tip.

ACKNOWLEDGEMENTS

We would like to thank Frank Barnett, Dave Robson and Mike Earnshaw for their invaluable technical and other help, and The Natural Environment Research Council for funding the project.

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ADIEU PROFESSOR

With the greatest sense of loss and sorrow we have to report the death of RICHARD ERIC HOLTTUM aged ninety-five.

His later years were affected by the death of his wife, his total deafness and, two years ago, severe bodily weakness with mental black-out and permanent loss of memory, all of which he bore with his characteristic dignity and fortitude. On the Fourteenth of October he was admitted to hospital with pneumonia and died resignedly and peacefully on the Eighteenth.

An *Obituary* is planned for *The Bulletin*.

REVIEWS

FERNS AND FERN ALLIES OF CANADA by William J. Cody and Donald M. Britton. 1989. 430 pp. Agriculture Canada, Publication A53-1829-1989E. ISBN 0-660-13102-1. Price: US \$38.50 (Canada), US \$46.20 (elsewhere), from Books Express, P.O. Box 10, Saffron Walden, Essex CB11 4EW (all countries except Canada and USA).

This is a definitive account of the ferns and allied plants of Canada by two professional botanists that have made pteridophytes their speciality. It has been a long time in the making and the authors have kept abreast of current thinking and referred to the latest paper on each species if it occurs. The 'Remarks' under each species make very interesting reading. The book is written however, for the interested layman and the initial chapters put topics like cytology, the role of hybrids, choice of latin names etc. into context.

I was pleased to see, after so much recourse to the alphabet in many recent regional accounts of ferns, that this book is arranged systematically, 12 families being included, the most interesting being the Adiantoid ferns being put with *Dennstaedtia* and *Pteridium*, a relationship not generally accepted now. At the generic level the names *Phyllitis* and *Camptosorus* are maintained and so, thankfully, is the name *Asplenium viride* Huds.; *Athyrium alpestre* (Hoppe) Rylands is retained for *A. distentifolium* Tausch, perhaps correctly so. It is interesting to see the differences between the North American taxon (subsp. *americana*) and our European plant. The evolutionary relationships of complex genera like *Dryopteris* (11 spp.) and *Polystichum* (11 spp.) are explained in detail. The correct name for *Azolla caroliniana* Willd. should be *A. filiculoides* Michx.

Each taxon is illustrated; the detailed drawings are good but some of the whole plant figures could have been treated with more care, or have too obviously been drawn from herbarium specimens. In such cases the 'jiz' of the plant is lost. The book ends with 159 detailed maps showing the distribution of all taxa in Canada, a really very useful adjunct. All in all, this is a good book and should be on the shelves of all interested in Northern hemisphere ferns.

A.C. JERMY

NEW ZEALAND FERNS AND ALLIED PLANTS by Patrick J. Brownsey and John C. Smith-Dodsworth. 1989. 176 pp plus 36 pp full colour. David Bateman, Auckland. ISBN 1-86953-003-9. Price: £40 from David Bateman Ltd, PO Box 100-242, North Shore Mail Centre, Auckland, N.Z.

This is an expensive book, but one, once seen, that all fern-lovers will want to possess. It covers 184 species of fern and 22 fern allies, including those introduced to New Zealand and now part of the flora. 216 of these are illustrated in beautiful colour pictures from which all species can be easily identified and most are elaborated in some 198 line drawings or black-and-white photos. I find the latter sometimes overprinted and quite dark, however. There are keys to the genera and, in the text, keys to the species. The descriptions are concise and details of distribution are given generally or more precisely for the rarer species. A map of the two islands is given at the back of the book with localities mentioned in the text. Common English, and Maori names, where available are given. The ecological notes give a good idea of the garden requirements of the species should the plant become available in Spore Exchange banks.

A.C. JERMY

CYTOTAXONOMIC NOTES ON THE PTERIDOPHYTES OF COSTA RICA 1. GLEICHENIACEAE

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ABSTRACT

Eight species of *Gleichenia* from Costa Rica have been cytologically investigated. Six of these represent new chromosome counts for the genus.

INTRODUCTION

The programme of research on the cytotaxonomy of the pteridophyte floras of two contrasting islands at opposite ends of the Caribbean was effectively brought to a close by the publication of the results for Jamaica (Walker 1962, 1966, 1973) and for Trinidad (Jermy 1985, Walker 1985, Jermy & Walker 1985). These surveys had raised a whole series of questions which made it desirable to extend the work to the mainland of tropical America and this culminated in a visit to Costa Rica in 1986 by A.C. Jermy and myself.

Costa Rica has an exceedingly rich fern flora whose individual species cover the entire spectrum from being narrow endemics to those which are widespread throughout tropical America or even beyond. Many genera are either not, or only very poorly represented in the Caribbean region whilst others are common there. Such a situation was ideal for the purpose of the present programme. Identification of the plants has been made infinitely easier by the publication by David Lellinger of the first part of his monumental *The ferns and fern-allies of Costa Rica, Panama, and the Chocó* in 1989.

MATERIALS AND METHODS

Meiotic fixations were made in 3 parts absolute alcohol to 1 part glacial acetic acid either directly in the field or a few hours later at base. Before leaving Costa Rica the acetic alcohol was replaced by 70% ethanol for storage until examination at Newcastle. Voucher specimens were routinely taken, together with additional ripe sporing material.

Living plants were sent to the Royal Botanic Gardens, Kew and to Moorbank Garden at Newcastle University. Spores were also collected and these have provided a valuable source of additional plants. Cytological work is still continuing on most families as new plants raised from spores become fertile. However, two families in particular neither transplant successfully without very special conditions nor can be raised easily from spores. These are Gleicheniaceae and the filmy ferns Hymenophyllaceae and the cytological results have been wholly dependent on field-fixed material. Work on these two families has now been completed and form the first two parts in the present series of reports.

RESULTS

The cytological results are given in Table 1.

TABLE 1

Cytologically investigated taxa of *Gleichenia* from Costa Rica

Taxon	Coll. No.	Locality	Chromosome Number	Ploidy
<i>G. bancroftii</i> Hook.	T14361	Cerro de la Muerte Pcia. S. José, 2000m	n = 56	2x (4x?)
<i>G. bifida</i> (Willd.) Spreng.	T14075	Santa Rosa, Pcia. Cartago, 565m	n = 34	2x

	T14118	Fila Esquinas, Pcia. Puntarenas, 2500m	n = 34	2x
	T14209, T14354	Zona Protectora, Pcia. Heredia, 700m	n = 34	2x
<i>G. costaricensis</i> (Underwood) C.Chr.	T14180	Volcan Poas, Pcia. Alajuela, 2500m	n = 68	4x
	T14377	Cerro de la Muerte, Pcia. S. José, 2500m	n = 68	4x
	T14418	Cerro de la Muerte, Pcia. S. José, 3100m	n = 68	4x
<i>G. intermedia</i> Bak.	T14363, T14364, T14366	Cerro de la Muerte, Pcia. S. José, 2000m	n = 34	2x
<i>G. nitidula</i> Rosenst.	T14036, T14048	Tausito, Pcia. Cartago, 1600m	n = 34	2x
<i>G. aff. nitidula</i>	T14058	Taucito, Pcia. Cartago, 1600m	n = 34	2x
<i>G. retroflexa</i> Bomm. & Christ	T14044	Tausito, Pcia. Cartago, 1600m	n = 34	2x
<i>G. strictissima</i> Christ	T14039, T14049, T14054, T14057	Taucito, Pcia. Cartago, 1600m	n = 34	2x

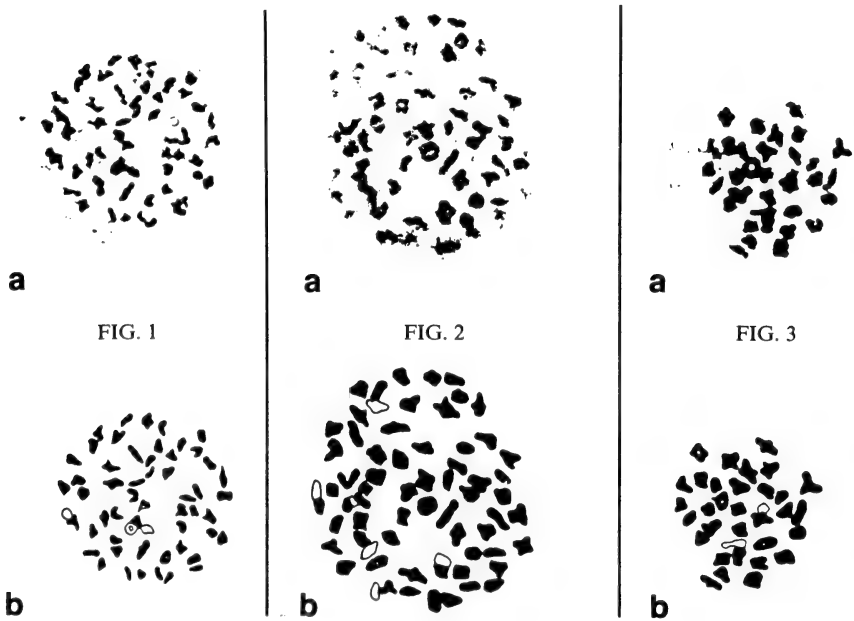


FIGURE 1: a) Metaphase I in *G. bancroftii*, x 1000. b) Explanatory diagram showing 56 bivalents.
FIGURE 2: a) Metaphas I in *G. costaricensis*, x 1000. b) Explanatory diagram showing 68 bivalents.
FIGURE 3: a) Metaphase I in *G. bifida*, x 1000. b) Explanatory diagram showing 34 bivalents.

NOTES ON SOME INDIVIDUAL SPECIES

G. bancroftii

This large handsome species is very distinctive, being the only member of the genus in the New World with one (up to 3) bipinnate primary branches which are not dichotomously forked. This is related to a small number of Old World species.

Although having a wide range from Mexico to Venezuela and including much of the Greater and Lesser Antilles this species is considered to be rather rare in Costa Rica. Lellinger (1989) noting the presence of only three specimens, two from Pcia. Heredia and one unlocalized. My cytologically worked specimen was from a new locality, namely the Cerro de la Muerte in Pcia. San José. I also photographed this unmistakable species in the Zona Protectora, Pcia. Heredia. The addition of two further localities in only a few weeks of random collecting suggests that *G. bancroftii* may be much more widespread in Costa Rica than had been realised.

Like the specimens from Jamaica (Walker 1966, 1973) and from Mexico (Mickel, Wagner & Chen 1966) the Costa Rican material showed $n = 56$. This agrees with the only other member of the subgenus which has been cytologically examined, namely *G. glauca* Hook. Further comments on the chromosomes of *G. bancroftii* will be found in the Discussion.

G. bifida.

This is one of the most widespread and abundant members of the tropical American gleichenias, ranging from Mexico to Brazil and throughout the Caribbean. It is a very characteristic plant of roadside banks and open clearings where it often forms dense thickets, frequently intermixed with other species of *Gleichenia*. The underside of the segments is covered by a dense tomentum of brown hairs which is rather variable as regards its density.

G. bifida has proved to be diploid with $n = 34$ wherever it has been examined, namely Jamaica, Puerto Rico, and Trinidad among the Caribbean islands and Mexico and now Costa Rica on the mainland (see Table 2 for references).

In Trinidad *G. bifida* was a member of a small complex of species and backcross hybrids involving *G. remota* (Kaulf.) Spreng. and *G. interjecta* Jermy and T. Walker, the latter being the fertile allotetraploid derivative of the cross *G. remota* \times *G. bifida*, followed by chromosome doubling. There relatively high proportions of hybrid plants were discovered in the course of random sampling of populations. Bearing these facts in mind a search was made in Costa Rica for hybrids involving *G. bifida* but none were found, although this may have been due to insufficient sampling in the time available or to the apparent absence of *G. interjecta*. It would be worth while to carry out a systematic search for this latter species as it may be formed *de novo*, independently of a Trinidadian source, since both parental species *G. bifida* and *G. remota* are present in Costa Rica and may be found growing together e.g. on a roadside bank west of Mogos, Pcia. Puntarenas at c. 100m altitude.

G. costaricensis

One of the three plants for which chromosome counts were obtained was gathered from the type locality of the species on a roadside bank on Volcan Poás, Pcia. Alajuela at c. 2500m. The other two plants were from the Cerro de la Muerte, Pcia. San José at 2500m and 3100m respectively. All three showed $n = 68$ and hence were tetraploid, the only species to be so in this survey of Costa Rican taxa. The bivalents are more or less uniform in appearance (fig. 2) and lack the marked bimodal size distribution seen in those of *G. interjecta* in Trinidad (Walker 1985).

G. nitidula

Two specimens from Tausito, Picia. Cartago, were diploid with $n = 34$, as was also a third one from the same locality. However, this third plant whilst initially being identified as *G. nitidula* on closer examination was found to differ from this species in some important features such as details of the bud scale morphology. This is probably a new taxon which will have to be described and named but in the meantime it is recorded in Table 1 as *G.aff. nitidula*.

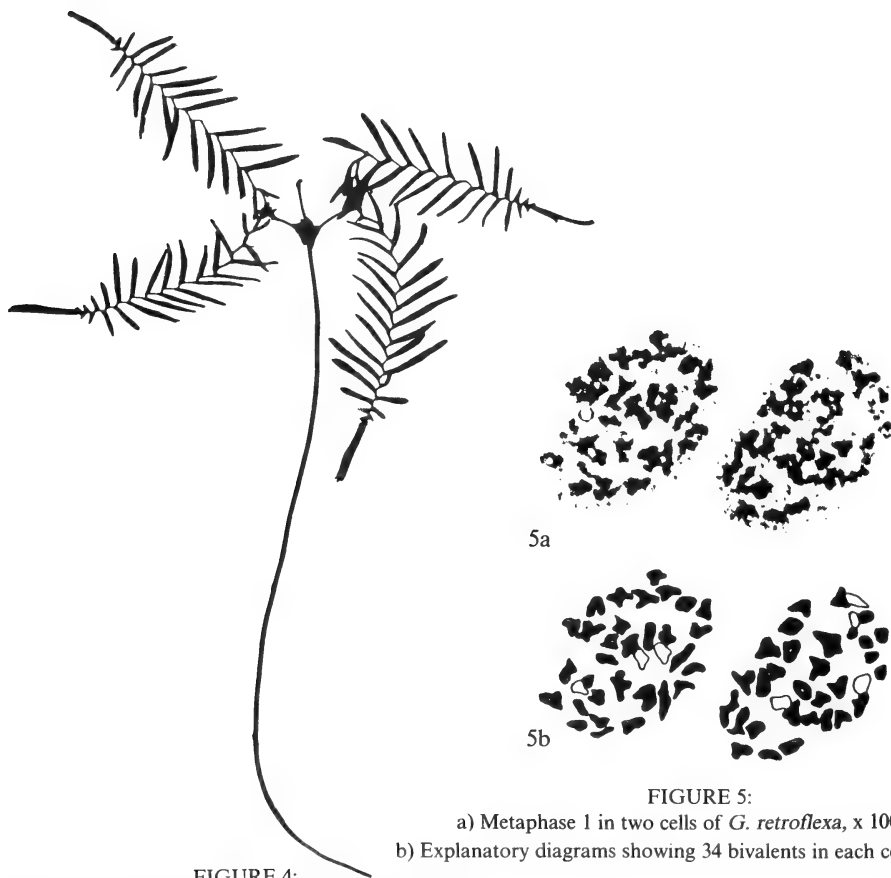


FIGURE 4:

Silhouette of frond of *G. retroflexa* c. half natural size.

G. retroflexa

This species is highly distinctive with its small stature and strongly reflexed widely spaced segments borne on axes having a characteristic zig-zag formation (fig. 4). Despite its anomalous appearance it is a member of subgenus *Mertensia* and is a diploid with $n = 34$ (figs. 5a, 5b). Luis Gomez (quoted in Lellinger 1989) considers that this species hybridizes with *G. intermedia*, the offspring being *G. orthoclada* Christ. It would be of great interest to examine this latter taxon cytologically to determine its alleged hybrid status, and if this is confirmed to see if it is a diploid hybrid between the two presumed parental species or if chromosome doubling has taken place to produce a fertile allotetraploid. It appears to be not uncommon in the Cordillera Central; if it is a diploid hybrid this suggests that it has been formed repeatedly.

DISCUSSION

Holtum's treatment (1957) of *Gleichenia* s.l. recognised the two genera *Gleichenia* and *Dicranopteris*, the former consisting of the three subgenera *Gleichenia*, *Diplopterygium* and *Mertensia* and the latter of two subgenera, namely *Dicranopteris* and *Acropterygium*. Each subgenus characteristically has its own distinctive basic chromosome number (Walker 1966). Although both subgenera of *Dicranopteris* are represented in Costa Rica no cytological results were obtained and as a consequence they will not be considered further here.

In *Gleichenia*, subgenus *Gleichenia* is absent from the New World in contrast to *Diplopterygium* and *Mertensia* which are present in both the eastern and western hemispheres. *Diplopterygium* consists of only a few species of which *G. bancroftii* is the sole American representative. As noted earlier the two species of *Diplopterygium* that have been examined, namely *G. bancroftii* in tropical America and *G. glauca* in India, both have $n = 56$ and in the lack of further information this has always been assumed to be the diploid state. The chromosome morphology of *G. bancroftii* is very distinctive, the bivalents appearing to be smaller and more attenuated than those of the other subgenera, particularly *Mertensia* (compare figures 1, 2 and 3). Whilst meiotic chromosomes cannot be used for karyotype analysis, nevertheless the difference in appearance between such chromosomes in these two subgenera suggests that karyotypic analysis of somatic cells may be very rewarding. Such an analysis in *Diplopterygium* may make possible a judgement as to whether the $n = 56$ represents a diploid level of ploidy on a base number of $x = 56$ or a tetraploid level on a base of $x = 28$, the latter figure fitting somewhat more easily into the known basic chromosome number series in the genus *Gleichenia*, namely $x = 20, 22, (28)$ and 34 .

By contrast *Mertensia* is a sizeable subgenus containing some 90 species in total of which c.40 occur in the American tropics and in southern South America (Tryon and Tryon 1982). The basic chromosome number, $x = 34$, is typical of all members throughout the world that have been counted (for records of the extra-American species see Löve, Löve and Pichi Sermolli 1977). In the New World a total of 6 species and 2 hybrids had been cytologically examined prior to the present communication (Table 2).

TABLE 2

Cytology of New World taxa of *Gleichenia* subgenus *Mertensia* prior to present communication.

Taxon	Country	Reference	Chromosome Number	Ploidy
<i>G. bifida</i> (Willd.) Spreng.	Jamaica	Walker (1966, 1973)	$n = 34$	2x
	Trinidad	Walker (1985)	$n = 34$	2x
	Mexico	Smith & Mickel (1977)	$n = 34$	2x
	Puerto Rico	Sorsa (1968)	$n = 34$	2x
	(Costa Rica)	pres. comm.	$n = 34$	2x)
<i>G. brittonii</i> (Maxon) C.Chr.	Trinidad	Walker (1985)	$n = 34$	2x
<i>G. interjecta</i> Jermy & T. Walker	Trinidad	Walker (1985)	$n = 68$	4x
<i>G. jamaicensis</i> C. Chr.	Jamaica	Walker (1966)	$n = 68,$ $2n = 136$	4x

<i>G. palmata</i> (Schaffn.) Moore	Jamaica	Walker (1966)	n = 34	2x
<i>G. × pseudobifida</i> Jermy & T. Walker	Trinidad	Walker (1985)	n = 34 1s, 34 11s	3x
<i>G. remota</i> (Kaulf.) Spreng.	Trinidad	Walker (1985)	n = 34	2x
<i>G. × subremota</i> Jermy & T. Walker	Trinidad	Walker (1985)	n = 34 1s, 34 11s	3x

The present work adds a further 6 species (Table 1) which, together with *G. bifida* represents about half the Costa Rican taxa of *Mertensia*. These new records consist of 5 diploid and one tetraploid species, bringing the total of New World taxa so far examined to 9 diploid and 3 tetraploid species, together with 2 triploid interspecific hybrids.

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NEW RECORDS AND NEW CYTOLOGICAL RESULTS FOR THE FERN FLORA OF MADEIRA

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ABSTRACT

Two taxa, *Asplenium adiantum-nigrum* and *A. × ticinense*, are recorded for Madeira for the first time. For these and for two other species (*A. septentrionale* and *Cheilanthes tinaei* for which no cytological data were given in the survey of the cytology of indigenous Madeiran ferns compiled by Manton et al. 1986) the chromosome numbers are reported. The rare *Hymenophyllum wilsonii* was found at two new localities; its identity was cytologically confirmed.

INTRODUCTION

In a study concerning the cytology of the fern flora of Madeira, chromosome numbers and/or meiotic pairing behaviour of chromosomes were reported for almost all indigenous species of the island (Manton et al. 1986). In subsequent publications, the chromosome number of *Anogramma leptophylla* from Madeira was documented (Gibby 1986) and three new endemic taxa whose cytology was already shown in the publication by Manton et al. (1986) were formally described and named (Gibby & Lovis 1989). The cytology of some fern species from Madeira that were known only from herbarium collections were not included in these papers.

Stimulated by the work of Manton et al. (1986), the authors of this contribution were able, during an excursion to Madeira in August 1988, to record two ferns as new to Madeira and to collect material for chromosome counts of two further species that had not yet been checked cytologically from this island.

MATERIALS AND METHODS

For examination and measurements of spores in the field a small portable microscope with calibrated eyepiece was used. This method (Bennert et al. 1990) allows identification of hybrids by their aborted spores directly in the field. Furthermore, different cytotypes of aggregate species (like *Asplenium trichomanes*) or diploid and tetraploid taxa belonging to closely related and morphologically very similar species complexes (like *Asplenium adiantum-nigrum* and *A. onopteris*) can be separated by spore measurements, provided that their size is sufficiently distinct. More exact measurements of spore size was done later using preparations mounted in balsam (Euparal) (see Bennert et al. 1989). For cytological investigations premature sporangia were fixed in the field using a mixture of acetic acid and ethanol (1:3). Preparations were made following the classical method of Manton (1950:293). Some plants were collected living and cultivated in Glotttartal or in the greenhouse of the Botanical Garden at Bochum for further investigations. For documentation, herbarium specimens of all new recorded taxa were collected (Ras = herbarium Rasbach; WB = herbarium Bennert).

RESULTS

A new endemic *Dryopteris* hybrid (most likely *D. aitoniana* × *D. maderensis*) will be described separately (Bennert et al., in prep.). We here present the new records and new cytological results:

***Asplenium adiantum-nigrum* L.**

This species was hitherto unknown from Madeira although Manton *et al.* (1986) already suspected its occurrence on the island. *A. adiantum-nigrum* is known from the Azores, the Canary Islands and the Cape Verde Islands (Fernandes 1984, Hansen & Sunding 1985, Manton *et al.* 1986). On 15 August 1988, climbing uphill from the hydro-electric plant "Faja da Nogueira" (above Porto da Cruz) to the "Levada da Serra", we saw repeatedly plants whose morphology (see fig. 1a) and spore size were indicative of *A. adiantum-nigrum*.

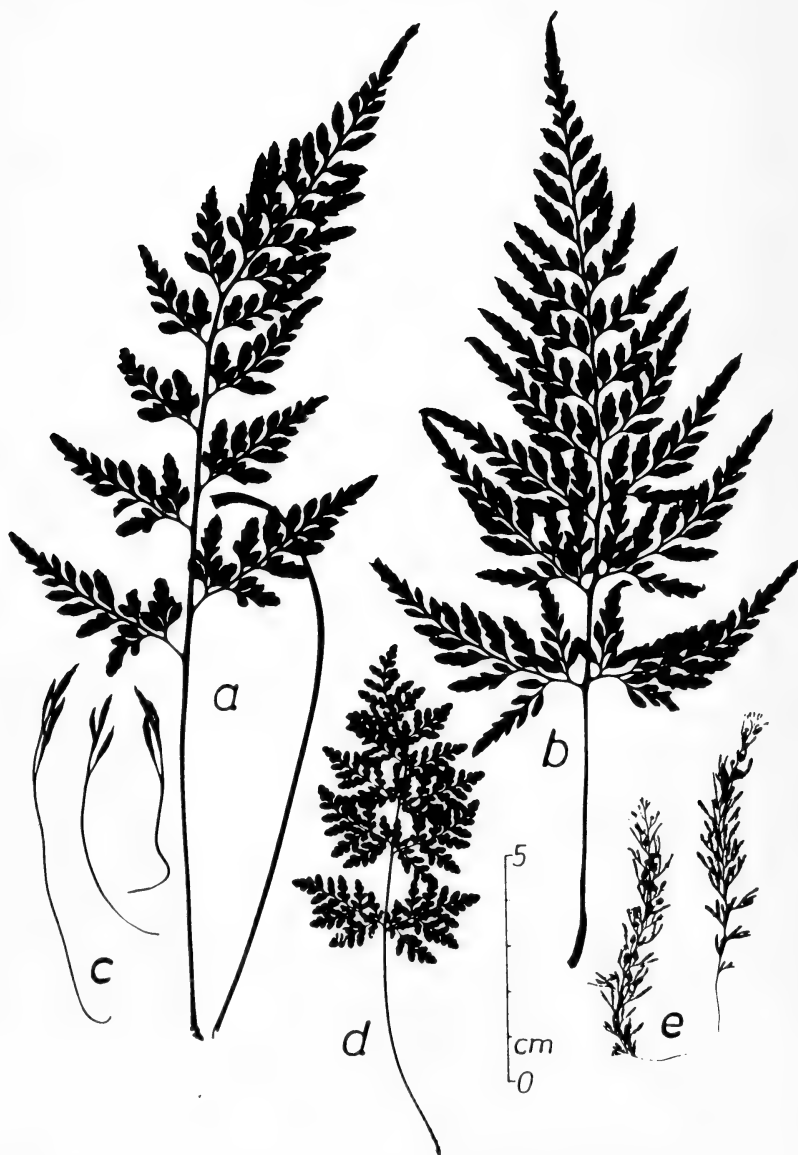


Figure 1. Silhouettes of fronds: a) *Asplenium adiantum-nigrum* (Ras-660), b) *A. x ticinense* (WB SP-27/88), c) *A. septentrionale* (Ras-638), d) *Cheilanthes tinai* (Ras-652), e) *Hymenophyllum wilsonii* (Ras-650).

The spore size (exospore without perispore) of several plants was measured and was in the range of (33) 36–40 (44) μm . This agrees well with the figures given by Reichstein (1984) for this species in Central Europe (in spite of slightly different methods applied for measurements). *A. adiantum-nigrum* grows between 600 and 900 m alt. preferring open situations and rocky outcrops in a laurel forest vegetation being rather heavily degraded by woodcutting and grazing. These sites are often dominated by seedlings of *Erica spec.* and several composites of which *Helichrysum foetidum* is the most notable one. Additional fern species noted include *Asplenium anceps*, *A. × ticinense* (see below), *A. onopteris*, *A. trichomanes* subsp. *quadrivalens*, *Polystichum setiferum* and *Pteridium aquilinum*.

One sample of *A. adiantum-nigrum* was fixed in the field (Ras-660); several specimens (Ras-655, 658, 660; WB 162/88, 164/88) and one living plant (SP 29/88) were collected. Cytological examination of Ras-660 showed that the plant was tetraploid with $n = 72^{II}$ at meiosis (fig. 2 a, 2b). For comparison, spores of *A. onopteris* were measured and a range of (25) 28–30 (33) μm was obtained. One plant (Ras-657) was checked cytologically; it was diploid and gave $n = 36^{II}$ at meiosis.

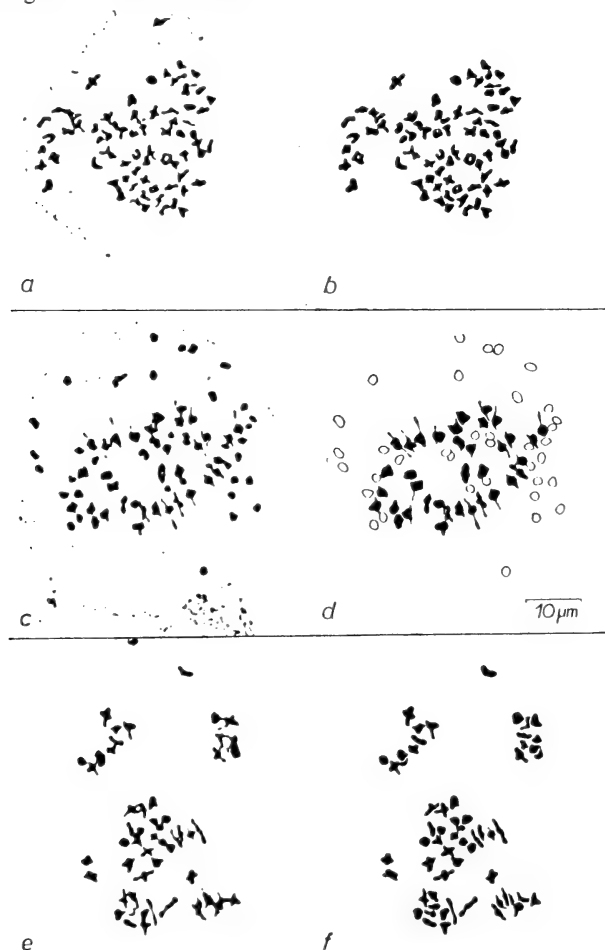


Figure 2. Cytology (spore mother cells in meiosis) of some Madeiran ferns. a) and b) *Asplenium adiantum-nigrum* (Ras-660), a) photograph, b) explanatory diagram showing 72 bivalents; c) and d) *A. × ticinense* (WB SP-27/88), c) photograph, d) explanatory diagram showing 36 univalents and 36 bivalents, pairs black, univalents outlined; e) and f) *Cheilanthes tinai* (Ras-652), e) photograph, f) explanatory diagram showing 60 bivalents.

Although occurring on all larger archipelagos of the Macaronesian Islands, *A. adiantum-nigrum* is, in contrast to *A. onopteris*, a rare plant with the exception of certain parts of the Azores (Fernandes 1984, Manton *et al.* 1986) where the climate tends to be cooler and moister than on most of the other islands. A chromosome count of a plant from the Azores by Queirós & Ormonde (1987) showed that it was indeed tetraploid thus confirming its identity with *A. adiantum-nigrum*. On Tenerife (Canary Islands) this species is obviously restricted to the highest parts of the island. It was found in the "Las Cañadas" at an elevation of ca. 2160 m in March 1979 by one of us (W.B.) and identified on the basis of spore size and perispore micromorphology (Bennert *et al.* 1982). A living plant from the same area ("Montaña Mostaza") was collected by D. Ludwig in November 1983 and since then cultivated in Bochum. It was checked cytologically by H.R. in September 1987 and found to be tetraploid.

***Asplenium* × *ticinense* D.E. Meyer**

Asplenium × *ticinense*, the hybrid between *A. adiantum-nigrum* and *A. onopteris*, was first described by Meyer (1960) based on a plant from Ticino (Switzerland). For the Macaronesian Islands this hybrid has, to our knowledge, only been mentioned by Fernandes (1984) who surveyed herbarium material of the *A. adiantum-nigrum* complex from the Azores and found several specimens with aborted spores.

On the way to the "Levada da Serra" where *A. adiantum-nigrum* and *A. onopteris* grew together (see above) several plants with intermediate morphology (see fig. 1b) and aborted spores were discovered. One living plant was collected (WB SP 27/88); it was found rather close to the "Levada da Serra" at an altitude of ca. 950 m. Two plants (Ras-659 and WB SP 27/88) were checked cytologically; as expected, they were triploid and showed $n = 36^{II}$ and 36^I at meiosis (fig. 2c and 2d). This result agrees fully with earlier cytological investigations of *A. × ticinense* (see Reichstein 1981). It corresponds with the genome formula $Cu\ On\ On$ with Cu representing one genome of *A. cuneifolium* and On one of *A. onopteris*. *Asplenium adiantum-nigrum* is an allotetraploid plant ($Cu\ Cu\ On\ On$) being derived from the two diploids, *A. cuneifolium* and *A. onopteris*. Thus, in *A. × ticinense* two genomes originating from *A. adiantum-nigrum* ($Cu\ On$) and one of *A. onopteris* (On) are combined with the two On genomes forming bivalents (in this case of allosyndetic origin) and the single Cu genome remaining unpaired.

***Asplenium septentrionale* (L.) Hoffm.**

Hansen & Sunding (1985) list this species for Madeira and the Canary Islands. Manton *et al.* (1986) mention a herbarium specimen from Madeira collected at "Passada da Vacas"; its cytology could not be checked. On 29 July 1988 we searched the area around the "Pico do Arieiro" (1818 m) and the "Pico do Juncal" (1800 m) for ferns. At an altitude of about 1760 m a colony of *Asplenium septentrionale* was found growing on steep NE exposed not shaded rocks. The following fern species were recorded in the vicinity: *Asplenium obovatum* subsp. *lanceolatum* = *A. billotii* (rare), *A. onopteris* (rare, only dwarfed plants), *A. trichomanes*, *Cystopteris* spec. and *Polystichum falcinellum* (dwarfed). Most plants of *A. septentrionale* were relatively small (see fig. 1c), the habitat was obviously rather dry. One plant (Ras-638) was fixed in the field (1 August 1988) and checked cytologically. It was tetraploid with $n = 72^{II}$. This result corresponds with earlier cytological investigations reported for this species in Europe and the Canary Islands (see Benl 1967 and Manton *et al.* 1986).

***Cheilanthes tinaei* Tod.**

Nardi *et al.* (1978) as well as Rasbach *et al.* (1982) report on herbarium specimens of this species from Madeira. The locality "São Roque" near Funchal, mentioned by Rasbach *et al.* (1982), had been visited by H.R. and K.R. in June 1980. A fixation of young sporangia

for cytological investigations gave no countable stages. On 4 August 1988 this colony growing on a wall of basaltic rocks just beside the road was revisited. The plants were completely dried out and blackened by exhaust gases and dust. One living plant was collected and has been cultivated since then as Ras-652 in Glottertal. The plant produced new growth (see fig. 1d) and could be checked cytologically. As expected, it was tetraploid and showed $n = 60^{II}$ at meiosis (fig. 2e and 2f). Not far away from the station of *Ch. tinaei* the occurrence of *Ch. maderensis* Lowe could be confirmed. Cytological control of a plant that was taken into cultivation showed $n = 30^{II}$, as it was already reported by Manton *et al.* (1986) for this species. *Cheilanthes guanchica* Bolle, another species reported to occur in the vicinity of Funchal (Rasbach *et al.* 1982), could not be found. Heavy traffic and intensive house building activities in Funchal are probably responsible for a strong reduction of the vegetation colonizing wall sides and will continue to affect these habitats adversely. So far, none of these *Cheilanthes* species have been found growing on natural rocks.

Hymenophyllum wilsonii Hook.

Manton *et al.* (1986) list a single station of this species in the western part of the island. In August 1988 we succeeded in discovering two new localities: 1) W of the "Boca da Encumeada" on a steep slope above rocks at the "Levada do Norte" at 1100 m alt., 2) E of the "Boca da Encumeada" at 1100 m alt., epiphytic on *Erica arborea*. A plant from one population (Ras-650, see fig. 1e) was controlled cytologically; it showed $n = 18^{II}$ at meiosis confirming its identity with *Hymenophyllum wilsonii*.

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THE FERN GAZETTE

VOLUME 13 PART 7

1990

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The new B.P.S. Centenary Ties are in dark green polyester material with the Centenary logo (without the words) in gold. The price is £6.50 plus £0.50 postage & packing; for members abroad, the postage & packing costs are £1.00. The ties will be sent as soon as possible, but this may be January.

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BRITISH PTERIDOLOGICAL SOCIETY

news sheet

1991 SUBSCRIPTIONS

DON'T FORGET the change in subscription rates for 1991! Payment is due by the **1st January 1991**. If you have not yet completed and returned a standing order form, please do so if at all possible. It would be a great help, to me and also to those of you who have trouble remembering when subscriptions are due! A S.O. form was sent to U.K. members with the *Pteridologist* and *Fern Gazette* in June, but further copies are available from me. If you do not wish to pay by this method, please send remittances to me in the next few months; cheques should be made payable to The British Pteridological Society. The *Bulletin* is the last publication you will receive for this year's subscription.

The new rates are:-

Full Personal Members	£12.50
Optional Members not receiving the <i>Fern Gazette</i>	£ 9.50
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Additional rates for airmail postage £4 for those receiving all journals, £2.50 for those not receiving the *Fern Gazette*. Remittances not made in sterling £3 extra.

Miss Alison M. Paul, Assistant Secretary (Membership), British Pteridological Society, c/o Botany Department, The Natural History Museum, Cromwell Road, London SW7 5BD.

INTERNATIONAL CENTENARY SYMPOSIUM - Pteridophyte Propagation and Culture

The response to the initial publicity for this event has been encouraging, with requests for further information coming from as far afield as Australia, U.S.A. and India. A varied programme is being planned which should appeal to anyone with a fascination for pteridophytes, no matter what their area or level of interest.

Eminent growers and scientists who it is hoped will be contributing include: D.E. Allen (U.K.), P.G. Barnes (U.K.), D.H. Brown (U.K.), G.J. Geldenhuys (S. Africa), C.H. Haufler (U.S.A.), E. Hennipman (Netherlands), B.J. Hoshizaki (U.S.A.), A.C. Jermy (U.K.), R.J. Johns (U.K.), D.L. Jones (Australia), J.T. Mickel (U.S.A.), M.H. Rickard (U.K.), T.G. Walker (U.K.) and P. Wyse-Jackson (Ireland).

Papers to be presented include several on the history of fern cultivation (e.g. the social history of ferns in Britain, ferns in gardens of the stately homes of Britain, living fern collections in Ireland), the diversity of cultivated ferns (e.g. *Davallia*, *Polypodium*, *Athyrium*), fern varieties in temperate Europe, commercial aspects (e.g. cultivation in Holland, culture and cropping of ferns in Canada, Florida and tropical America, micropropagation), and conservation, the role of the NCCPG and the future.

The programme will also include a visit to the living fern collections and the micropropagation unit at the Royal Botanic Gardens, Kew.

The second and final circular will be sent out shortly to those who have made an initial enquiry. Anyone who has not yet indicated a possible interest in the Symposium should write for further information to: **Jennifer Ide, Roehampton Institute, Whitelands College, West Hill, Putney, London SW15 3SN.**



MEETINGS PROGRAMME FOR 1991 - Provisional Summary

2 March	Spring Indoor Meeting - The Natural History Museum, London
21-24 May	Chelsea Flower Show: B.P.S. Stands
8-9 June	Weekend Meeting - Yorkshire Dales
22-23 June	Weekend Meeting - Radnorshire
7-11 July	International Symposium on the Propagation and Culture of Pteridophytes - London
12-18 July	National Tour of British Fern Gardens
13 July	Competitive Fern Show - Pebworth
4-10 August	Week Meeting - Isle of Skye
16-18 August	Southport Flower Show: B.P.S. Stand
13-14 September	Harrogate Horticultural Show: B.P.S. Stand
19-25 September	Centenary Week Field Meeting - Cumbria
12 October	Autumn Indoor Meeting - Royal Botanic Gardens, Kew

This is a provisional list to help people with their diaries for next year! Full details will appear with the Bulletin in the usual way.

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A NEW PUBLICATION



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NOTEWORTHY SPECIES OF GRAMMITIDACE FROM SOUTH-EAST ASIA B.S.PARRIS



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Royal Botanic Gardens, Kew
iv+129pp., incl. 31 figs
Size 245 x 155 x 8 mm

£10.00
Paperback 1990
ISBN 0 9504876 8 6

SAMPLE ENTRY

TABULA 3996

27. PROSAPTIA CAPILLIPES

Prosaptia capillipes (C. Chr.) Copel. in Philip. J. Sci. 81(2): 117 (1953).

Polypodium capillipes C. Chr. in Brittonia 2(4): 310 (1937). Type: Papua New Guinea, Central Province, Wharton Range, Murray Pass, Brass 4731 (holo. BM!).

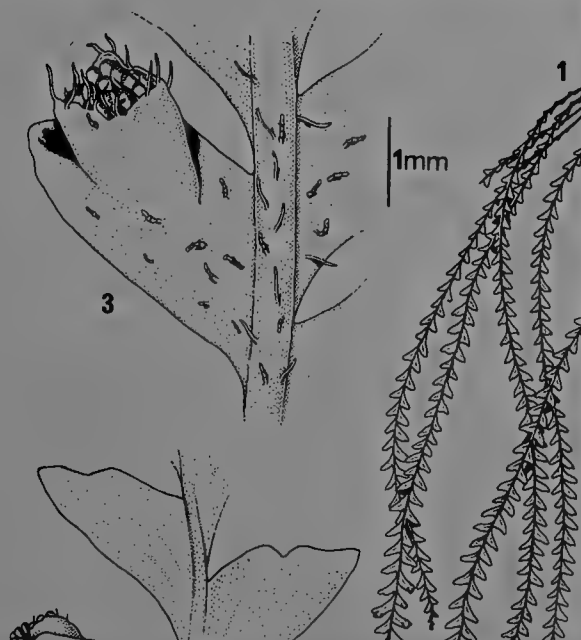
Rhizome long-creeping; rhizome scales dark brown, narrowly lanceolate, with deciduous concolorous simple eglandular marginal hairs, apex of scales either hair-tipped or gland-tipped. Fronds up to c. 3 mm apart, stipes articulated to rhizome on pedicels c. 2 mm tall, c. 0.5-6 cm (Christensen, 1937b, says 8 cm simple eglandular narrowly elliptic pinnate, the sterile less oblong, sometimes on the stipe, present around the mouth simple eglandular occasionally on the upper surface of the or less at right angle section, and up to groups of three or sporangia glabrous

Material seen:

PAPUA NEW GUINEA
46217 (K); Mt. S
Edward, Brass 44
Murray Pass, Wharton
61772 (K); Isuani
Victoria, 1889, Macgregor

HABITAT. A pen-
montane forest or
subalpine grassland
RANGE. Restrict

3996





CENTENARY TOUR OF FERN GARDENS IN BRITAIN

JULY 1991

The tour in its original form is unfortunately not viable due to insufficient support.

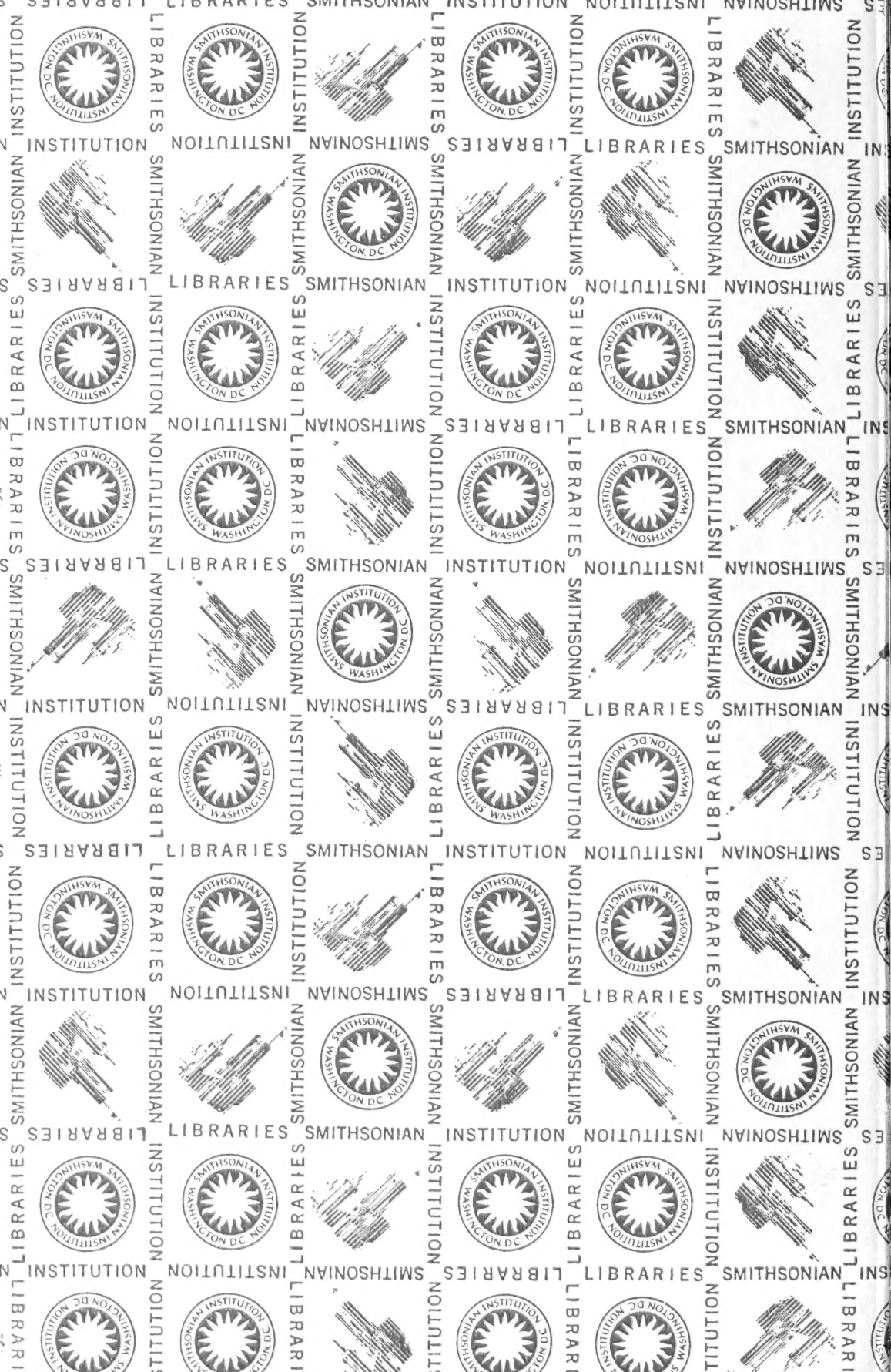
There has, however, been some interest in an abbreviated tour, so it has been decided to offer instead a three day tour. Starting and finishing in London, it will run from Friday 12th July to Sunday evening 14th July. The tour will include the Fern show at Pebworth (Worcester) and four or five of the best Fern gardens in Britain. The cost is likely to be £150 per person with a £20 supplement for single rooms.

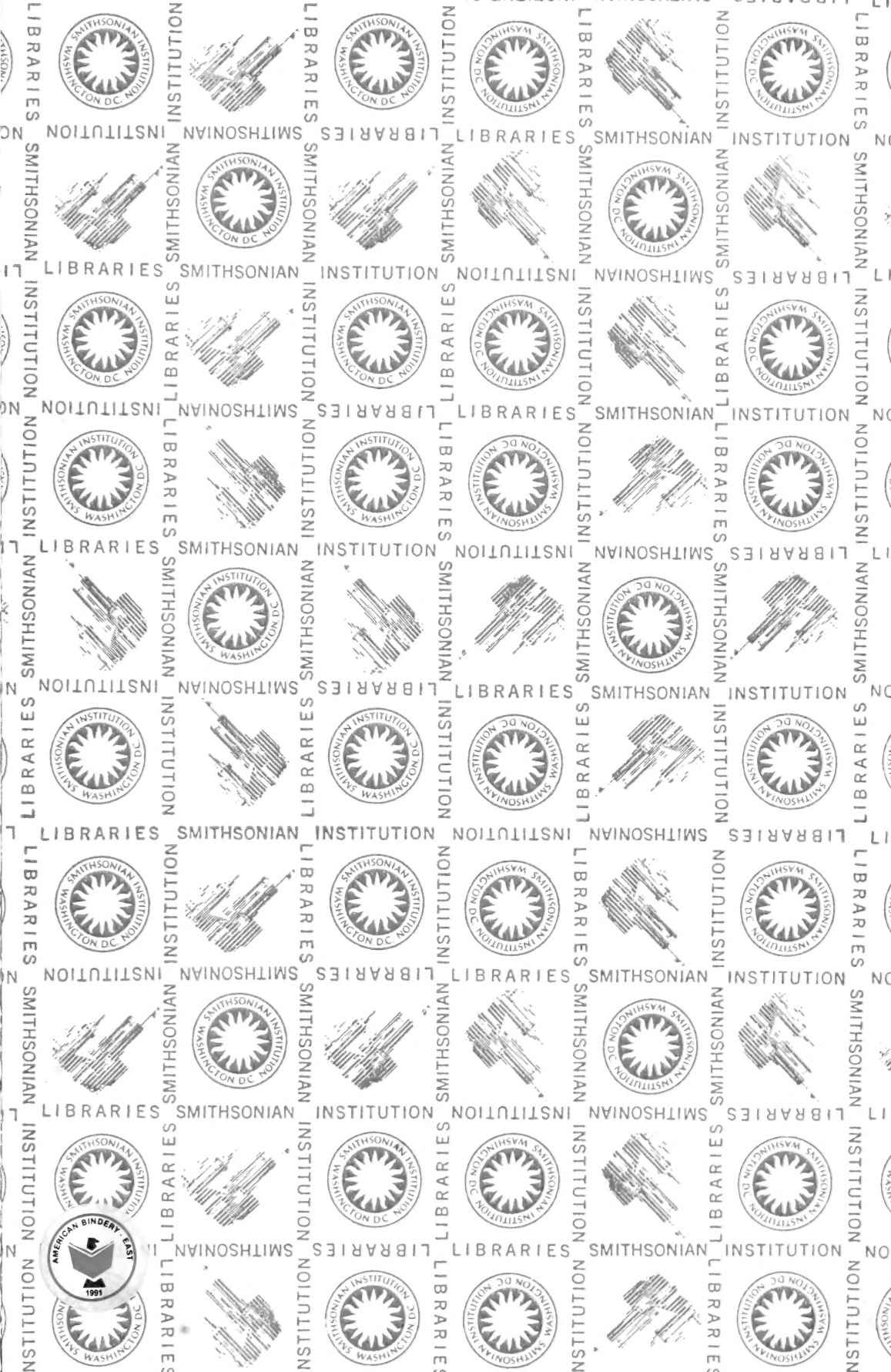
All people who have expressed an interest in the original week long tour will automatically receive information on the shorter one. Any additional members wishing to join this new tour should please contact Martin Rickard, The Old Rectory, Leinthall Starkes, Ludlow, Shropshire, SY8 2HP as soon as possible. All interested parties will be kept informed of progress. Full details will be circulated, with the booking forms, early in the new year.

= The Society very much regrets any inconvenience which may have been caused by this change of plan.









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